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VOLUME 60
1973

ANNALS OF THE
Missouri Botanical Garden

Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.
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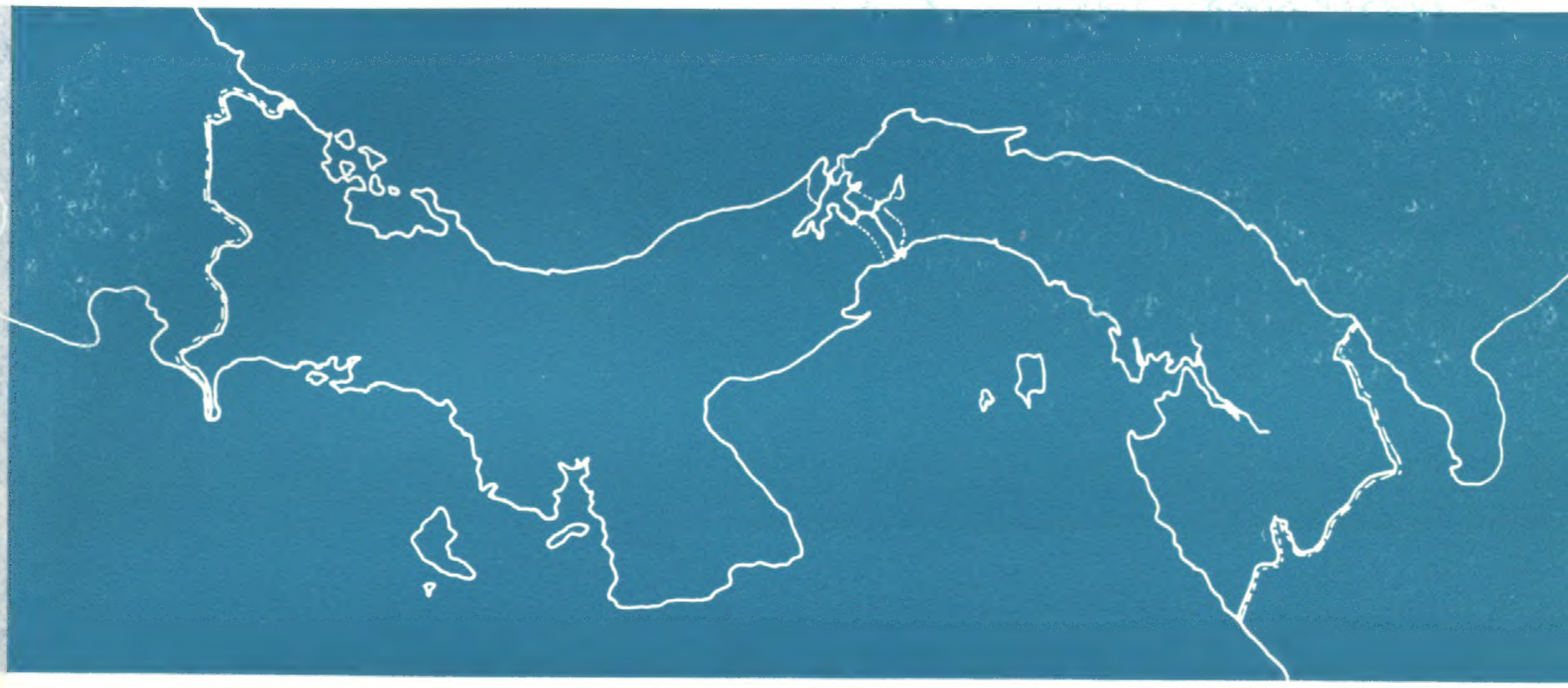

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The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden. Papers originating outside the Garden will also be accepted. The ANNALS appears three times a year, and three numbers, totaling about 400 pages, constitute a volume.

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ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

VOLUME 60
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NUMBER 1

ANNALS OF THE
Missouri Botanical Garden

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part II

FAMILY 3B. NAJADACEAE[1]

W. ALAN WENTZ[2] AND ROBERT R. HAYNES[3]

Plants herbaceous, annual or rarely perennial, aquatic, submersed in fresh or brackish waters, monoecious or dioecious. *Stems* slender, much branched, rooting at the lower nodes; lower internodes elongate, the upper internodes reduced. *Leaves* subopposite or appearing whorled because of reduced internode length, sessile, each divided into lamina and auricle; laminas linear and flattened, 1-nerved, the margins usually serrulate; auricles variously shaped, each enclosing a pair of tiny hyaline scales, the auricle margins usually spiny-toothed. *Flowers* axillary, sessile, solitary or clustered, each usually enclosed in a membranous involucre, the perianth absent; staminate flowers each consisting of a single stamen, the anthers 1- or 4-thecate, dehiscing vertically, the filaments at first short, elongating slightly at anthesis; carpellate flowers each consisting of a single 1-ovuled carpel, the placentation basal, the styles solitary, each divided into 2–4 subulate stigmatic lobes. *Fruit* achene-like, the pericarp closely enveloping the seed, areolate; seeds without endosperm, areolate.

A monogeneric family of probably fewer than 40 species, widespread in both hemispheres; two species, *Najas arguta* H.B.K. and *N. guadalupensis* (Spreng.) Magnus are known to occur in Panama.[4] *Najas* is very important as a food source

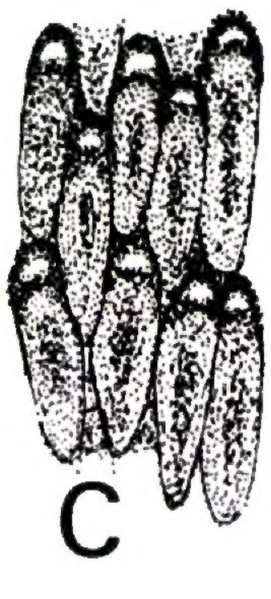
---

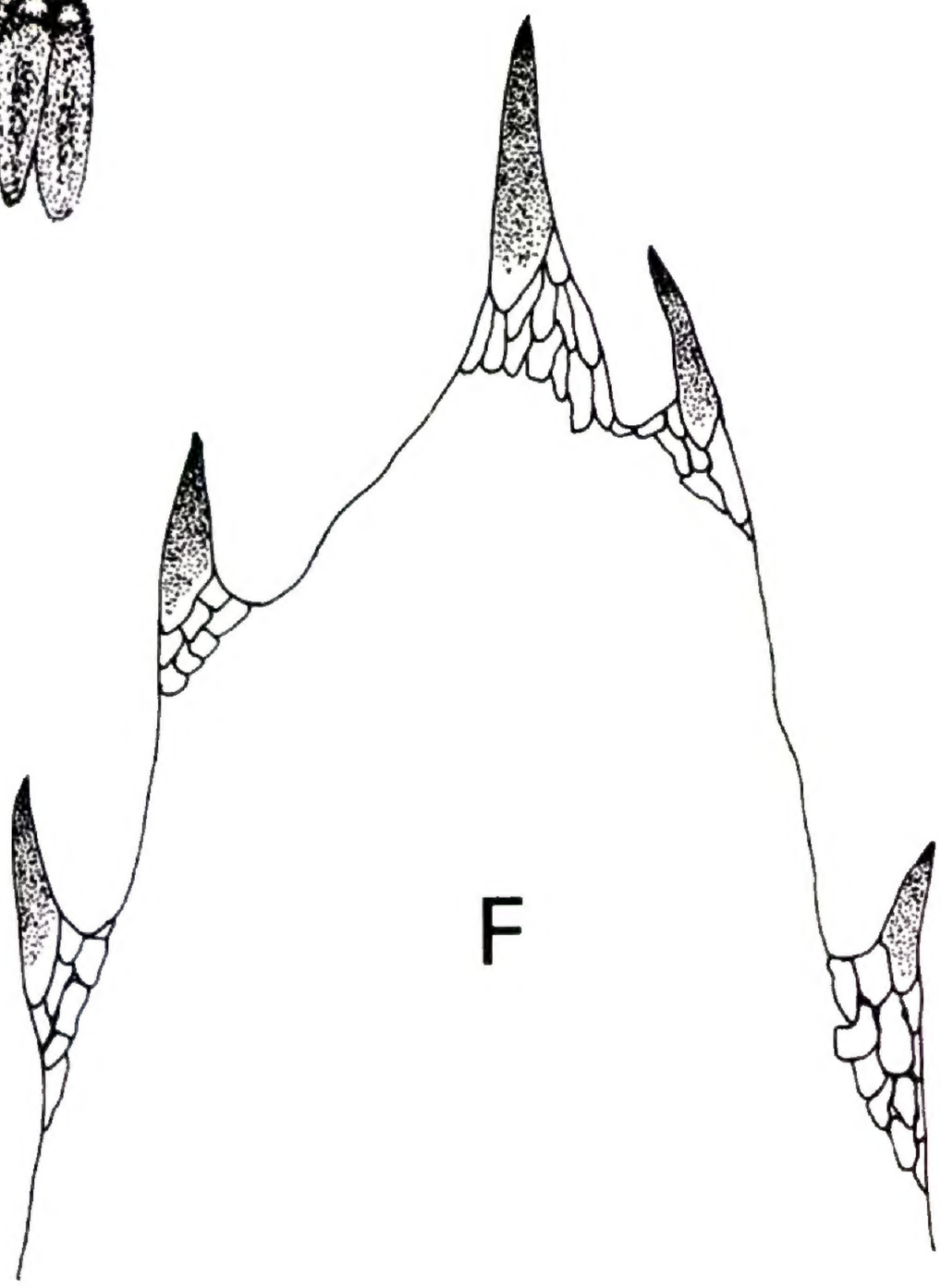
[1] Contribution from the Botany Program (Paper No. 844) and the Herbarium of Ohio State University, Columbus, Ohio 43210.

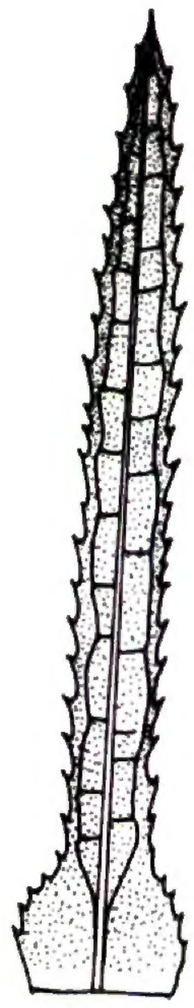
[2] Department of Botany, 1735 Neil Avenue, Ohio State University, Columbus, Ohio 43210. *Present address:* School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48104.

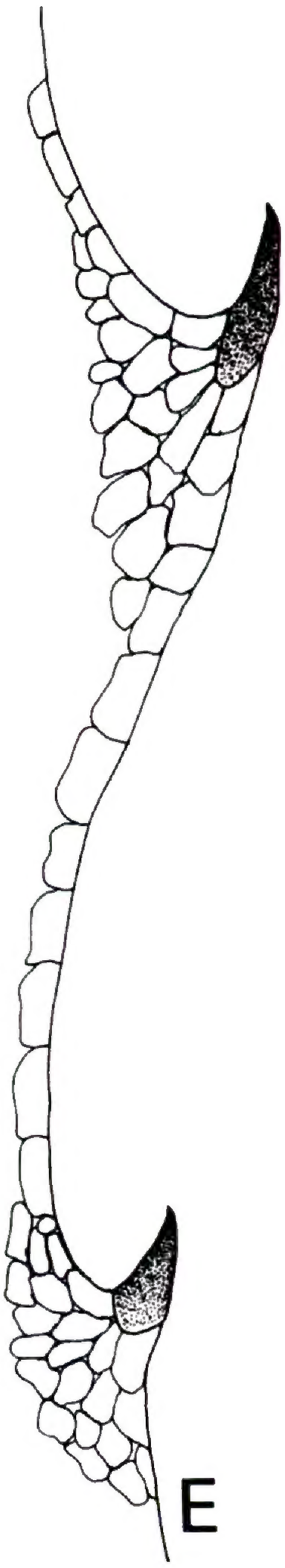
[3] Department of Botany, 1735 Neil Avenue, Ohio State University, Columbus, Ohio 43210.

[4] After this paper had gone to press, one fragment of *Najas marina* L. was found in a packet attached to a specimen of *Syringodium filiforme* Kütz., Potamogetonaceae [SAN BLAS: Caledonia Harbor, Mt. Vernon, 26 April 1939, *Elmore L38* (NY)]. For descriptions and illustrations of *N. marina* see R. W. Butcher, *A New Illustrated British Flora* 2: 629. 1961, and D. S. & H. B. Correll, *Aquatic and Wetland Plants of Southwestern United States*, pp. 125–126. 1972.









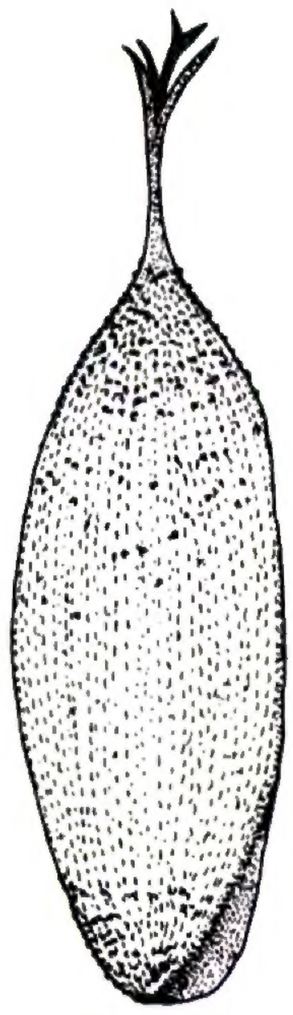


FIGURE 1. *Najas arguta* H.B.K.—A. Habit (× ½).—B. Carpellate flower with involucre (× 30).—C. Section of pericarp wall showing areolae (× 75).—D. Leaf (× 2½).—E. Leaf margin (× 62).—F. Leaf apex (× 62). [After *Duke 8310* (OS).]

for many vertebrates and as a breeding area for fishes and invertebrates. In tropical and subtropical areas, members of the genus often clog canals and waterways.

The fruits of the Najadaceae have traditionally been considered to be achenes or nutlets. However, *Najas* fruits can not correctly be referred to either of these fruit types since both are, by definition, "dry fruits." *Najas* fruits are similar to achenes in all respects except that, in the natural state, the fruits seldom remain viable when dry. We have therefore designated the fruits as "achene-like" until a better name is proposed for fruits of this type.

1. NAJAS

Najas L., Sp. Pl. 1015. 1753.

Caroliana Raf., Jour. Phys. Chim. Hist. Nat. Arts 89: 259. 1819.
Caulinia Willd., Mem. Acad. Roy. Sci. Hist. (Berlin) 87. 1798.
Fluvialis Adans., Fam. Pl. 2: 472. 1763.
Hyas Dumort., Anal. Fam. Pl. 61. 1829.
Ittnera C. C. Gmel., Fl. Bad. 3: 590. 1808.

Characters of the family.

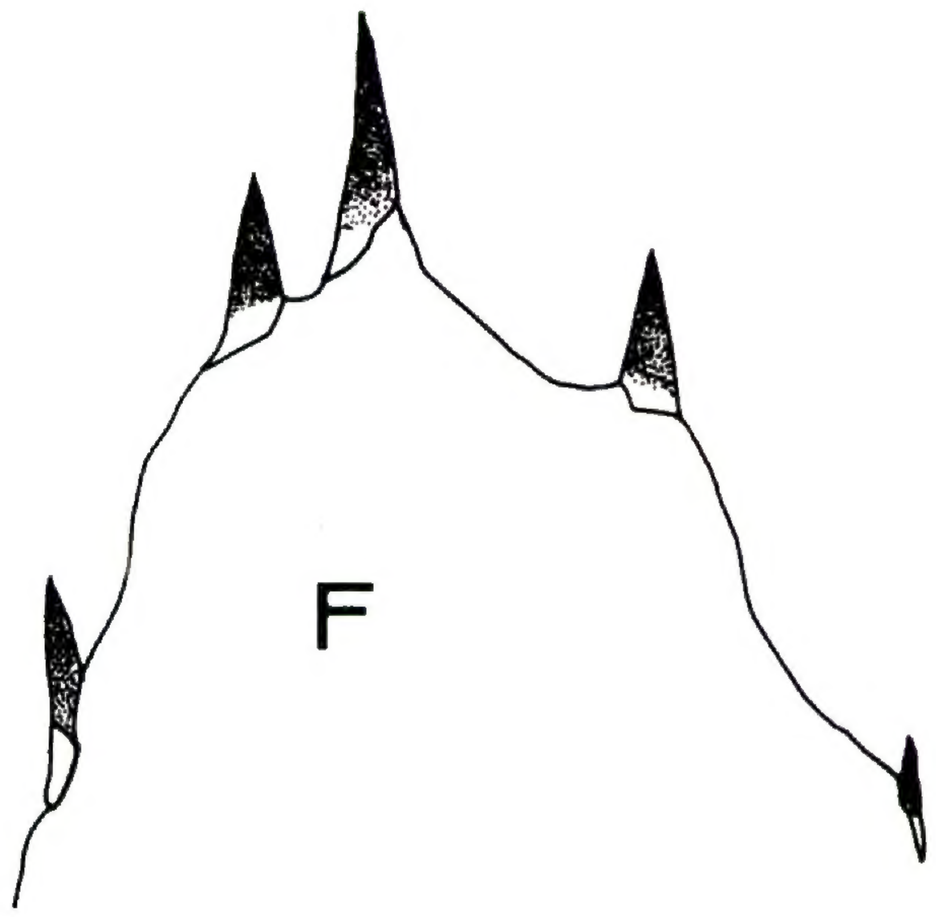
a. Fruit longer than 2 mm; pericarp wall appearing papillose; fruit areolae longer than broad; seeds with 3 dark bands; laminas conspicuously serrulate, the teeth multicellular, fewer than 25 per side; auricles conspicuously broader than the laminas, the teeth smaller than the lamina teeth ..... *N. arguta*

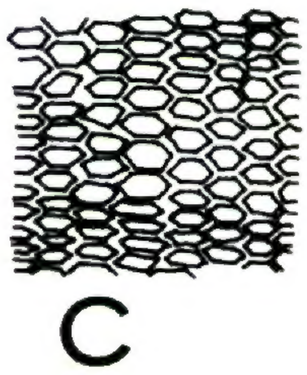
a. Fruit shorter than 2 mm; pericarp wall not appearing papillose; fruit areolae broader than long; seeds with 2 dark bands; laminas inconspicuously serrulate, the teeth unicellular, ca. 100 per side; auricles scarcely broader than the laminas, the teeth larger than the lamina teeth ..... *N. guadalupensis*

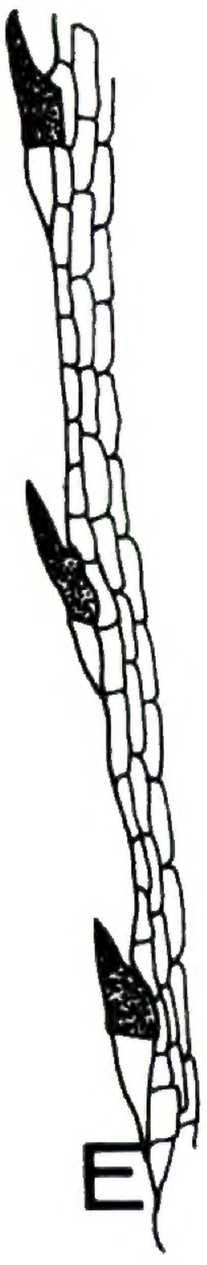
1. **Najas arguta** H.B.K., Nov. Gen. and Sp. Pl. 1: 371. 1815.

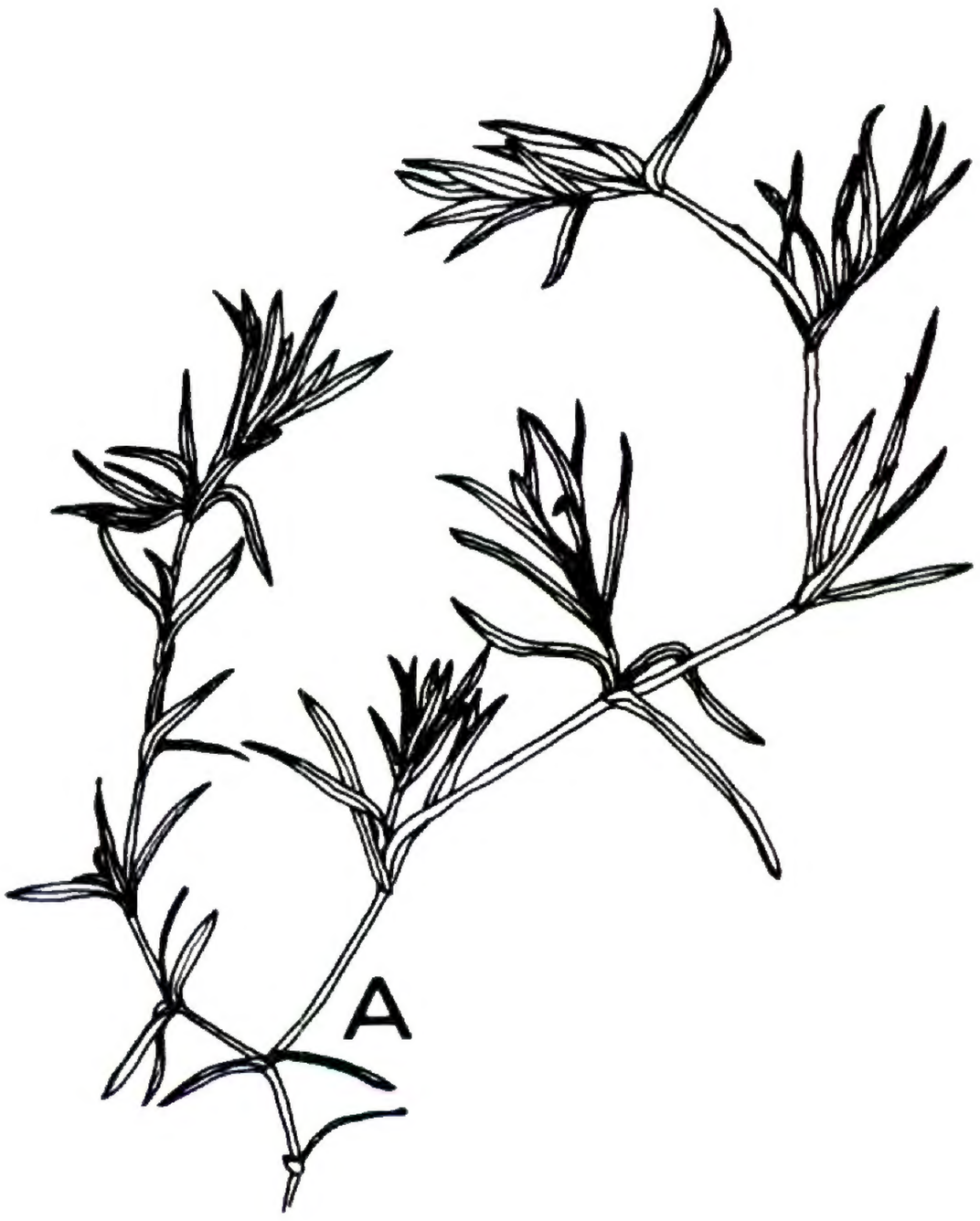
N. tenera Schrad., Gött. Gel. Anz. 2: 715. 1821.
Caulinia tenella C. G. Nees *in* Neuwied, Reise Bras. 2: 345. 1824.

Plants glabrous, monoecious. *Stems* 0.3–1.0 mm in diameter, profusely branched, in habit appearing bushy; lower internodes elongate (to 13.5 cm long), the upper internodes shortened (to 7 mm long or less). *Leaves* 1.2–2.8 cm long; laminas 0.6–1.9 mm wide, acute to acuminate, mucronate, conspicuously serrulate with 15–25 teeth per side, the mucro slightly larger than the lateral teeth, the teeth multicellular, formed by layers of cells decreasing in cell number outward, terminated by a large, sharp-tipped cell; auricles 1.2–3.4 mm wide, wider than the laminas, round to truncate, serrulate with 2–7 teeth per side, the teeth similar in structure to but smaller than those of the laminas. *Flowers* solitary, the staminate in the upper leaf axils, the carpellate in the lower leaf axils, the involucre purple-tinged; staminate flowers 2.0–2.2 mm long, the involucre above the anther abruptly narrowed into a short beak (0.5 mm long), ending in 4 sharp-tipped lobes, the anther to 1.6 mm long, 1-thecate, the filament at anthesis to 1.2 mm long; carpellate flowers 1.7–2.1 mm long, the involucre above the ovary abruptly narrowed into a short beak ending in 3–4 sharp-tipped lobes, the style ending in 2 stigmatic lobes that extend above the involucral beak. *Fruit* 2.1–2.6 mm long and 0.6–0.8 mm wide, yellowish-white, elongate-fusiform, with a single









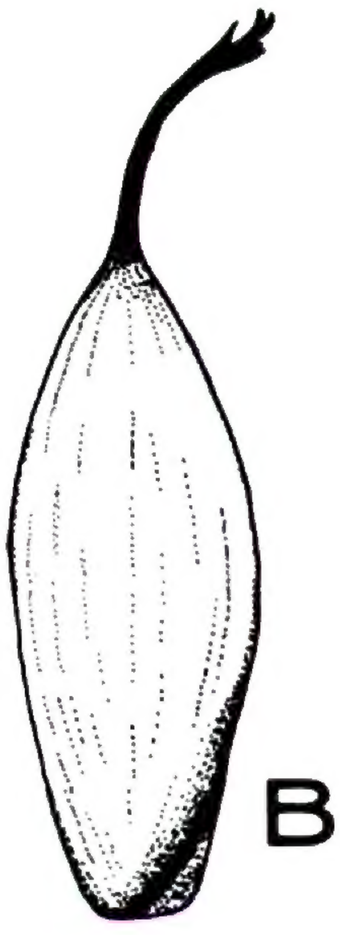


FIGURE 2. *Najas guadalupensis* (Spreng.) Magnus—A. Habit (× ½).—B. Carpellate flower with involucre (× 38).—C. Section of pericarp wall showing areolae (× 85).—D. Leaf (× 2).—E. Leaf margin (× 62).—F. Leaf apex (× 62). [After *Lazor, Tyson & Loftin 2690* (FSU).]

basally flattened keel-like rib along which the involucre splits, the areolae sometimes inconspicuous, longer than broad, to 0.2 mm long and ca. 0.05 mm broad, in ca. 50 longitudinal rows, the end walls raised giving the pericarp wall a papillose appearance; seeds elongate-fusiform, greenish-white with 3 dark bands.

CANAL ZONE: Chagres River, *Dwyer & Robyns 76* (MO, US), *Fairchild 2102* (GH, MO); at Juan Mina, *Trapido B1022* (GH, NY, UC, US); ca. 2 mi. above Pan Canal, *Lazor & Boreham 2913* (FSU, UC); mouth of Río Moja Polla, near village of Las Guacas, *Trapido B1021* (MO, NY). Gamboa, *Tyson, Dwyer & Blum 4602* (FSU, MO). Gatun Lake, *Duke 8310* (OS). Madden Lake, *Woodson & Schery 956* (MO). DARIÉN: Río Pirre, *Duke & Bristan 8310* (MO).

2. **Najas guadalupensis** (Spreng.) Magnus, Beitr. Gatt. Najas 8. 1870.

Caulinia guadalupensis Spreng., Syst. 1: 20. 1825.

Plants glabrous, monoecious (?). *Stems* 0.3–0.8 mm in diameter, profusely branched; lower internodes elongate (to 4 cm long), the upper internodes shortened (to 5 mm long or less). *Leaves* 1.2–2.8 cm long; laminas 1.2–1.8 mm wide, acute, mucronate, minutely serrulate with ca. 100 teeth per side, the mucro and 2 subterminal teeth larger than the lateral teeth, the teeth unicellular; auricles to 1.9 mm wide, barely wider than the laminas, only slightly flared below, with usually 7 teeth on the upper half of each side, none below, the teeth similar in structure to but larger than those of the laminas. *Flowers* solitary, the involucre light green with brown streaks; staminate flowers not seen; carpellate flowers to 1.5 mm long, the involucre above the ovary abruptly narrowed into a short beak, usually ending in 3 sharp-tipped lobes, the style ending in 2–3 stigmatic lobes that extended above the involucral beak. *Fruit* 1.2–1.6 mm long and 0.4–0.6 mm wide, yellowish-white, fusiform, with a single basally flattened keel-like rib along which the involucre splits, the areolae inconspicuous, broader than long, to 0.2 mm long and 0.6 mm wide, (4–)6-angled, in ca. 20 longitudinal rows; seeds fusiform, greenish-white with 2 dark bands.

Our examination of specimens from all parts of the Western Hemisphere indicates that *Najas guadalupensis* is a highly variable taxon. Further research may indicate that infraspecific taxa should be recognized or that this complex should be considered as several closely related species. Clausen (Rhodora 38: 333–345. 1936) and Ooststrom (Rec. Trav. Bot. Neerl. 36: 705. 1939) have reached similar conclusions. Several names have been proposed in apparent reference to this group, but at present, we have chosen the conservative approach in designating the Panamanian material as *N. guadalupensis*.

BOCAS DEL TORO: United Fruit Company boat landing ca. 4 mi. E of Changuinola on the Changuinola River, *Lazor, Tyson & Loftin 2690* (FSU).

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Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part II

FAMILY 5A. HYDROCHARITACEAE

C. DEN HARTOG[1]

Annual or perennial *marine or fresh-water herbs*, having either a creeping monopodial rhizome with roots at the nodes and distichously arranged leaves, or an erect main axis with roots at the base and spirally arranged or verticillate leaves. *Leaves* submerged, sometimes floating or partly emerged, linear, lanceolate, elliptic, ovate, or orbicular, either sessile and then sometimes sheathing basally, or differentiated into blade and petiole; main veins more or less parallel, straight or curved, connected by perpendicular or ascending cross-veins; ligule absent; stipules sometimes present; squamulae intravaginales present. *Flowers* regular, or rarely slightly irregular (*Vallisneria*), unisexual, sometimes with rudiments of the other sex present, or bisexual, sessile or pedicellate, solitary or in cymose inflorescences, enclosed by a pedunculate or sessile spathe of 2 free or partly to completely connate spathal leaves; perianth of 1 or 2 whorls of 3 free segments; stamens (2–)3–several, arranged in 1 or more whorls, the anthers basifixed, 2- or 4-thecate, dehiscent lengthwise, the filaments more or less slender, sometimes absent; gynoecium paracarpous, (2–)3–15-carpelled, the ovary inferior, linear, ellipsoid, or ovoid, 1-loculed, the placentas parietal, either protruding nearly to center of the ovary or obsolete, the ovules several, orthotropous to anatropous, erect or pendulous, the styles (2–)3–15, often more or less split into 2 stigmatic branches, a long filiform hypanthium often occurring between the ovary and perianth. *Fruits* indehiscent, opening by decay of the pericarp, or rarely stellately dehiscent, the pericarp fleshy or membranous; seeds several, fusiform, ellipsoid, ovoid, or globose, the embryo straight, either with the hypocotyl and cotyledon not distinctly separated and with an inconspicuous plumule at the base of a lateral groove, or with a well differentiated hypocotyl and cotyledon and a large well developed plumule, endosperm absent.

The family consists of 14 genera with about 100 species and is widely distributed in the tropical and temperate areas of the world. Three genera, *Hydrilla*, *Thalassia*, and *Halophila*, occur in Panama.[2]

Useful references:

Hartog, C. den. The Sea-grasses of the World. Pp. 213–268. 1970.

Hutchinson, J. The Families of Flowering Plants. Ed. 2. Vol. 2. Pp. 538–541. 1959.

---

[1] Rijksherbarium, Schelpenkade 6, Leiden, The Netherlands.

[2] The key to genera is only applicable to material from Central America.

a. Caulescent fresh-water plants; upper and middle leaves opposite or in whorls of 3–8, not differentiated into petiole and blade, 1-nerved, at most 4 cm long; tannin cells present ..... 1. *Hydrilla*

aa. Marine plants with creeping rhizomes.

b. Leaves distichous, linear, sheathing basally, 9–17-nerved, to 60 cm long; tannin cells numerous ..... 2. *Thalassia*

bb. Leaves arranged in pairs or in a pseudowhorl, differentiated into a short petiole and an elliptic or ovate blade, to 2.5 cm long, 3-nerved, connected by ascending cross-veins; tannin cells absent ..... 3. *Halophila*

1. HYDRILLA

Hydrilla Rich., Mém. Cl. Sci. Math. Inst. Natl. France 12(2): 9, 61, 73, *t.* 2 (upper part). 1814.

Hydrospondylus Hassk., Flora 25, Beibl. 2: 33. 1842.

Perennial, submerged *fresh-water herbs*, with an erect main axis, rooting basally, the roots unbranched, smooth, the stem slender, unbranched or slightly to moderately branched. *Leaves* not differentiated into blade and petiole, linear or lanceolate, rarely elliptic, translucent, green, with many tannin cells, acute apically, the margin serrate, with 1 medium nerve, at most 4 cm long, the lower alternate or in whorls of 3, usually reduced in size, the middle and upper in whorls of 3–8; squamulae intravaginales 2, minute, fringed. *Inflorescences* axillary, sessile or subsessile, 1-flowered; spathe of 2 connate bracts. *Flowers* unisexual, the plants dioecious; staminate spathe subsessile, globose, dorso-ventrally flattened, with subulate appendages and a minute central knob; staminate flower freely-floating, pedicellate, the sepals 3, ovate to oblong-elliptic, strongly convex, reflexed, the petals 3, linear to spatulate, narrower than the sepals, spreading to reflexed, the stamens 3, the anthers erect, 4-thecate, latrorsely dehiscent; carpellate spathe sessile, tubular, bifid, membranous; carpellate flower sessile, with a long hypanthium, the sepals 3, oblong to obovate, convex, the petals 3, spatulate, narrower than the sepals, the ovary linear, unilocular with 3 parietal placentas, the ovules several, ortho- to anatropous, the styles 3, filiform to subulate, entire. *Fruits* linear, cylindrical; seeds cylindrical, glabrous, 2–6 in a row.

A monotypic Old World genus, introduced into Panama. The habit of *Hydrilla* is similar to that of *Elodea*. In fact, there is not a single vegetative character which gives an absolute distinction between the two genera.

1. **Hydrilla verticillata** (L. f.) Royle, Ill. Bot. Himal. *Pl. 376*. 1839.[3]—FIG. 1.

Serpicula verticillata L. f., Suppl. 416. 1781.
Udora verticillata (L. f.) Spreng., Syst. 1: 170. 1825.
Vallisneria verticillata (L. f.) Roxb., Fl. Ind., ed. Carey. 3: 751. 1832.
Elodea verticillata (L. f.) F. Muell., Key Syst. Vict. Pl. 1: 423. 1888.

Stems branched. *Leaves* with the lower in whorls of 3, linear to linear-lanceolate, sometimes obovate, the lowest sometimes alternate, 5–14 mm long and 1–1.5 mm wide, the middle and upper in whorls of 3–8, linear-lanceolate, acute, serrate, 10–25(–40) mm long and 1–2 mm wide; squamulae intravaginales 2, axillary, oblong, membranous, transparent, fringed, to 0.5 mm long. *Staminate spathe* solitary in the leaf-axil, 1.25–1.5 mm high, tearing open when the flower is

[3] Complete synonymy for this taxon is given in den Hartog (1970).

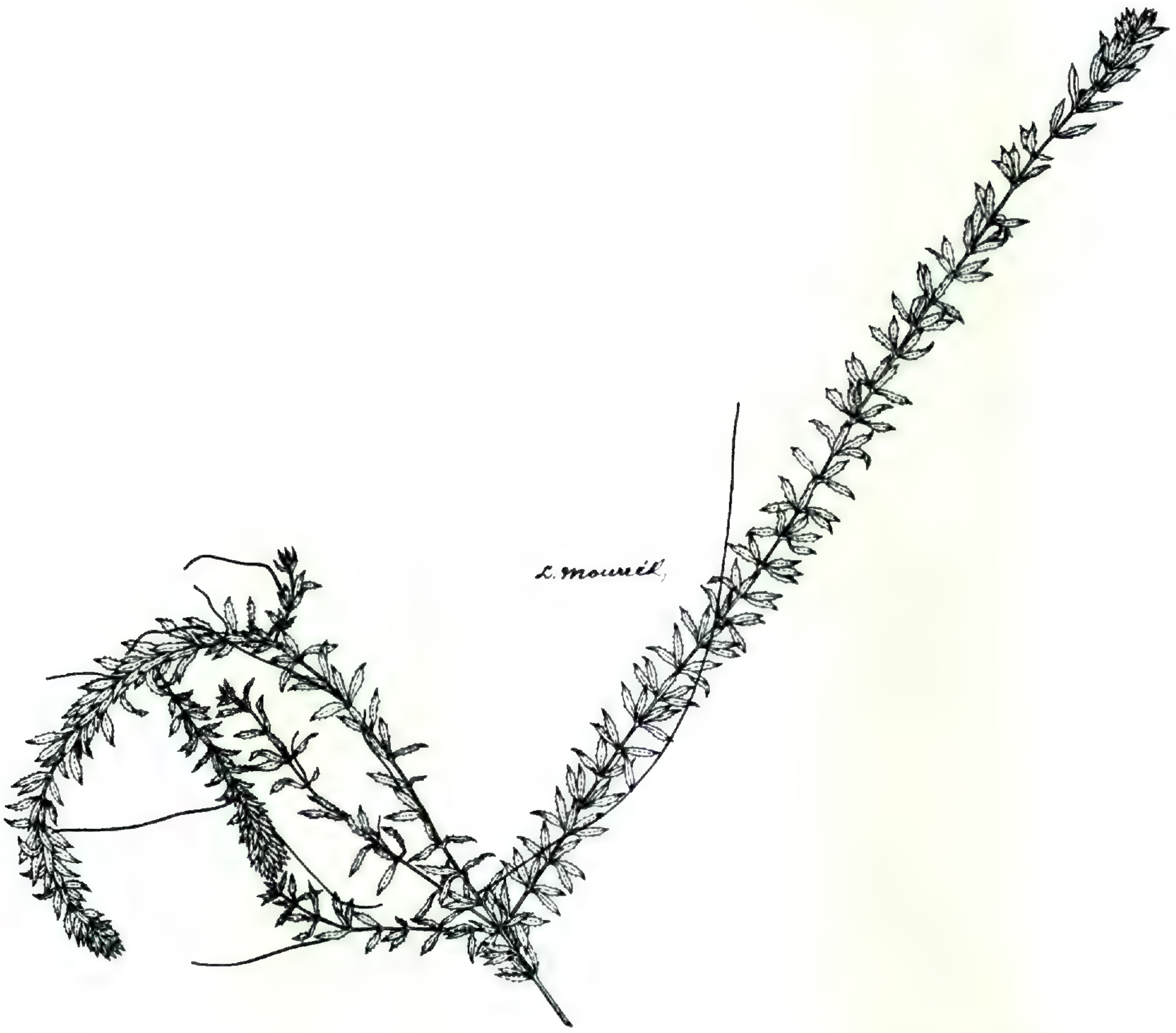

FIGURE 1. *Hydrilla verticillata* (L.f.) Royle, habit (× 1¼). [After *Dwyer & Robyns 75* (MO).]

released; pedicel 1–2 mm long; sepals white, often tinged with red, 1.5–3 mm long and 1 mm wide; petals white, often tinged with red, 2–3 mm long and 0.5 mm wide, falling before the sepals; stamens with slender, short filaments and linear anthers. *Carpellate spathe* ca. 5 mm long; sepals white, sometimes with red dots, 1.5–3 mm long and 0.75 mm wide, petals white, 1.5–3 mm long and 0.3–0.5 mm long; hypanthium 1.5–10 cm long; ovary 3–4 mm long, the styles 0.8–1 mm long. *Fruits* elongate, with a constriction between each pair of seeds, 4–7 mm long, surrounded basally by the remnants of the spathal bracts and bearing the remnant of the hypanthium (1.5–3 cm long) apically; seeds 2–6, in a row, cylindrical, oblong, apiculate at one side, 2–3 mm long, the testa smooth, dark brown.

Widely distributed in the Old World, from southern and eastern Europe, Africa, southern and eastern Asia, to Australia. The records from Panama are the first from the Americas.

CANAL ZONE: Barro Colorado Island, extremely abundant around edges of Gatun Lake, *Croat 7946* (MO). Chagres River, *Dwyer & Robyns 75* (MO). Chagres River at Colon Highway bridge, *Lazor & Tyson 3046* (MO). Gamboa, Panama Canal Company Dept. of Sanitation Boat Dock, *Lazor 3493, 3494* (both MO).

2. THALASSIA

Thalassia Banks *ex* König, Ann. Bot. (König & Sims) 2: 96. 1805.

Schizotheca Ehrenb. *ex* Solms *in* Schweinf., Beitr. Fl. Aethiop. 1: 194, 246. 1867.

Dioecious *marine herbs*, with numerous tannin cells; rhizome monopodial, terete; internodes short, with fine longitudinal grooves; roots 1 at each node, short, unbranched, with longitudinal air channels, densely set with fine root-hairs; scales membranous, 1 at each node. *Leaves* 2–6, distichously arranged on short, erect lateral shoots, linear, often somewhat falcate, differentiated into a green blade and a pale basal sheath, obtuse and finely serrulate apically, the margin entire, the main veins 9–17, parallel, joining the intramarginal veins near the apex, many fine longitudinal air channels and short brown tannin cells parallel with the veins. *Inflorescences* pedunculate, 1–2 on the staminate plants, 1 on the carpellate, always 1-flowered; spathal leaves of the staminate plants connate only on 1 side, those of the carpellate connate on both sides. *Staminate flowers* shortly pedicellate; tepals 3, elliptic; stamens 3–12, the anthers subsessile, light yellow, oblong, erect, (2–3–)4-thecate, lengthwise latrorsely dehiscent. *Carpellate flowers* subsessile; tepals 3; gynoecium 6–8 carpelled, the ovary muricate, 1-loculed or imperfectly 2- or 3-loculed, with a long partly persistent hypanthium, the placentas parietal, protruding far toward the center of the ovary, the styles 6–8, each split into 2 filiform stigmas 2–6 times as long as the style, each with 2 longitudinal grooves on the underside. *Fruits* globose, echinate, beaked, the fleshy pericarp bursting into a number of irregular stellately spreading valves; seeds few, ca. 8–10 mm long, conical with a thickened basal portion, the testa fugacious; embryo with a large hypocotyl, corresponding with the conical part of the seed, a cotyledon forming the thickened basal rim, the plumule small, pressed against the hypocotyl, the primary root rudimentary.

A genus of two closely related species, one occurring in the West Indies and the other in the tropical parts of the Indian and western Pacific Oceans.

1. **Thalassia testudinum** Banks *ex* König, Ann. Bot. (König & Sims) 2: 96. 1805.

T. vitrariorum Pers., Syn. Pl. 2: 563. 1807.—FIG. 2.

Herbs with rhizomes 3–6 mm thick, the internodes 4–7 mm long; roots with longitudinal air channels, the latter with septa at intervals of 1 mm. *Leaves* distichously arranged on short lateral branches arising from the rhizome at intervals of 5–19 internodes, obtuse and sometimes emarginate apically, slightly serrulate near the apex, the margin entire, 10–60 cm long, 4–12 mm wide, the main veins 9–15, connected by perpendicular cross-veins at intervals of about 1 mm; the transition between the blade and the sheath marked by a straight or a downward curved line; sheath 6–10 cm long, sometimes slightly auriculate. *Inflorescences* with the peduncle in the staminate 3–7.5 cm long, in the carpellate 3–4 cm long; spathal leaves oblong-elliptic, obtuse, serrulate, persistent, 1.5–3 cm long and 0.5–0.75 mm wide, with many short brown tannin stripes, the carpellate spathe usually only 1.5–2 cm long. *Flowers* with the pedicel of the staminate

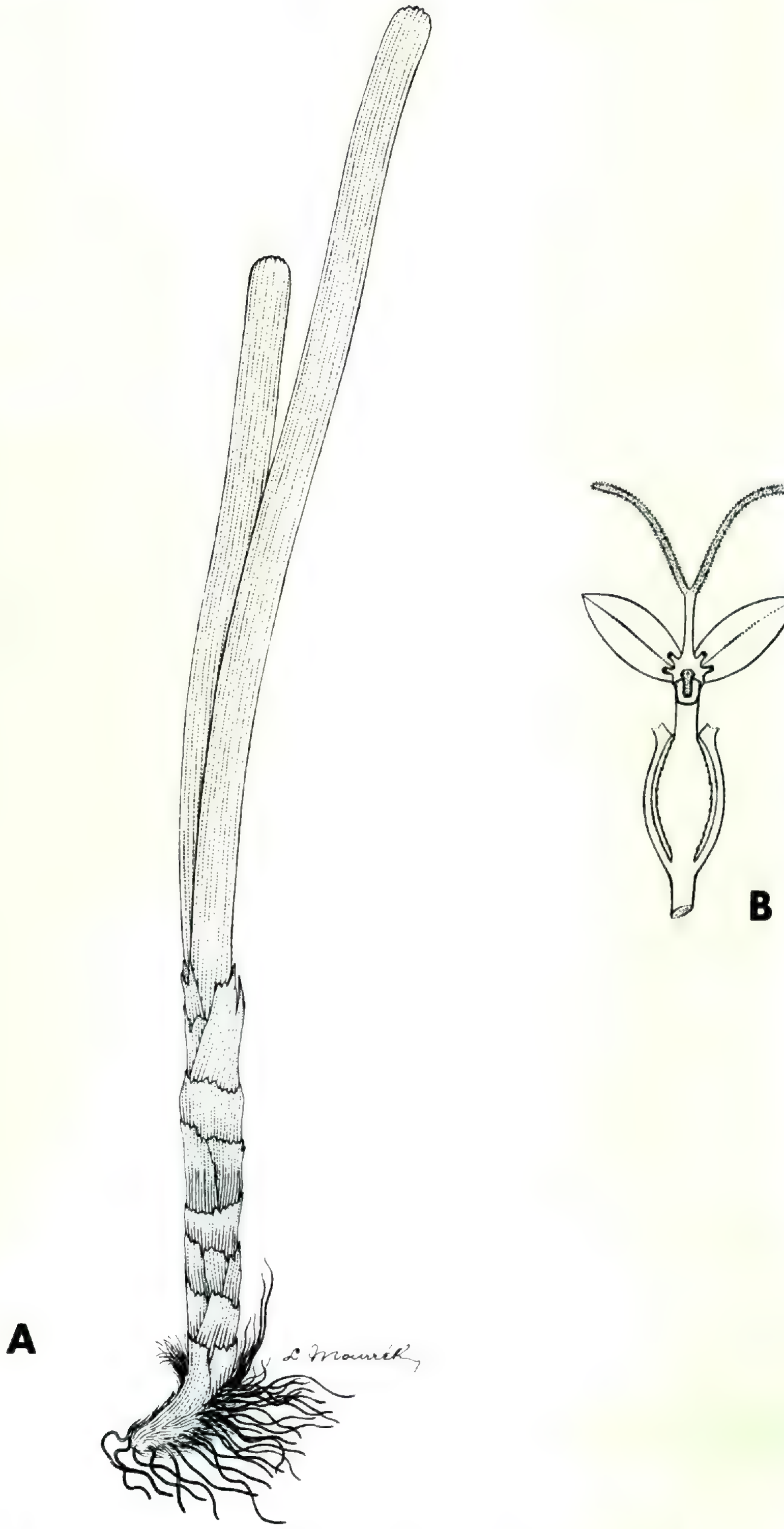

FIGURE 2. *Thalassia testudinum* Banks *ex* König—A. Habit (× ¾). [After *Johnston 1512* (MO).]—B. Flower. [After Orput & Boral, Bull. Marine Sci. 14: 298, *t. 10.* 1964.]

12.5–25 mm long, the carpellate subsessile, after anthesis shortly pedicellate; tepals uncolored, with numerous pink to violet spots and streaks (tannin cells), elliptic to ovate, obtuse to truncate and often toothed apically, spreading or recurved, 10–12 mm long and 4–4.5 mm wide, stamens 9, the anthers oblong, 8–9 mm long and 1 mm wide; ovary conical, 1 cm long, the hypanthium ca. 2 cm long, styles 7–8, 1.5–2.5 mm long, stigma 10–13 mm long, shed after flowering. *Fruits* ellipsoid to globose, roughly echinate, bright green to yellow green, sometimes red, 1.5–2 cm long and 2–2.5 cm wide, the beak 4–7 mm long, splitting into 5–8 irregular valves; seeds (1–2–)3(–6), pyriform, 10 mm long and 8 mm wide.

Widely distributed in the Caribbean and the Gulf of Mexico, northward to Cape Kennedy, Florida, and Bermuda.

CANAL ZONE: Toro Point, in shallow relatively quiet saltwater pools, behind coral-reefs, *Johnston 1512* (MO). SAN BLAS: Caledonia Harbor, Mt. Vernon, *Elmore L 29* (AHFH).

3. HALOPHILA

Halophila du Petit Thouars, Gen. Nov. Madag. 2: 2. 1806.

Monoecious or dioecious *marine herbs*, tannin cells absent; rhizome monopodial, creeping, rooting at the nodes with 1 or a few unramified roots closely set with fine root-hairs; 2 scales at each node, 1 embracing the rhizome, the other embracing an erect, lateral, often undeveloped shoot bearing the leaves (rarely with another 2 scales on the erect shoot below the leaves). *Leaves* paired, in pseudo-whorls or distichously arranged, sessile or petiolate, linear, lanceolate, oblong-elliptic, or ovate, entire or serrulate, rarely with scattered trichomes, a new shoot appearing between the leaves bearing scales, 1 or more pairs of leaves, and an inflorescence. *Inflorescences* with the spathe sessile, of 2 overlapping free membranous bracts, elliptic or obovate to suborbicular, acute or rounded to emarginate or indented, keeled, the keel sometimes serrulate, the margin entire, rarely ciliate or serrulate. *Flowers* unisexual, solitary, rarely 1 staminate and 1 carpellate flower in 1 spathe; staminate flowers pedicellate, the tepals 3, imbricate, the stamens 3, alternating with the tepals, the anthers sessile, 2- or 4-thecate, dehiscing lengthwise and extrorsely; carpellate flowers sessile or subsessile; ovary ellipsoid or ovoid, 1-loculed, with a long hypanthium crowned by the 3 reduced tepals apically, placentas parietal, protruding slightly into the ovary, the styles linear, 3–5. *Fruits* ovoid or globose, rostrate, 1-loculed, the pericarp membranous, seeds few to numerous, globose or subglobose; embryo of a well-developed large hypocotyl and a cotyledon of similar size, the plumule in the center of the depression at the chalazal end of the hypocotyl, sheathed by the expanded base of the cotyledon, the cotyledon spirally coiled upon itself, the primary root absent.

Widely distributed in all tropical seas, extending also into subtropical and even into warm-temperate waters. Of the eight species, two are known to occur in Panama.

a. Erect lateral shoots 1–10 mm long, with 2 basal scales, and bearing 1 pair of leaves; leaves with scattered stiff trichomes; plants monoecious ..... 1. *H. decipiens*

aa. Erect lateral shoots 6–40 mm long, with 2 basal scales and 2 further scales ca. halfway up, and at the top a pseudo-whorl of 4–6 distinctly petiolate leaves; leaves glabrous; plants dioecious ---------- 2. *H. baillonis*

1. **Halophila decipiens** Ostenf., Bot. Tidsskr. 24: 260. 1902.

H. baillonis auct. non Aschers. *ex* Dickie *in* Hook. f., Jour. Linn. Soc. Bot. 14: 317. 1874.
H. decipiens var. *pubescens* den Hartog, Fl. Males. I. 5: 411. 1957.

Monoecious *herbs*, the rhizome thin, fragile, with 1 root at each node, the internodes 1–4.5 cm long, the scales transparent, obovate, keeled, 3–7 mm long, hairy on the outside, incised apically, amplexicaul basally; lateral shoots 1–10 mm long, with only 1 pair of leaves. *Leaf-blades* oblong-elliptic, obtuse or rounded apically, cuneate basally, the margin finely serrulate, bright green, with short rigid unicellular trichomes on one or both sides, rarely glabrous, 10–25 mm long and 3–6 mm wide, cross-veins 6–9 pairs, ascending, joining the intramarginal veins which run ca. 0.5 mm from the margin, the midrib uniting at the apex with the intramarginal nerves; petioles triquetrous, 3–15 mm long. *Inflorescences* with the spathe ovate, acuminate, keeled, scarious, transparent, 3–4 mm long, the margin ciliate, the keel covered with fine serrulate teeth, with or without trichomes on the outside, containing 1 staminate and 1 carpellate flower, splitting at the top as the fruit ripens; the spathal leaf enclosing the carpellate flower embracing the other spathal leaf. *Staminate flowers* with the pedicels 3 mm long, the tepals oblong-elliptic to ovate, obtuse, convex, 1–1.5 mm long, the anthers ca. 1 mm long, after anthesis the complete flower with its pedicel breaks off. *Carpellate flowers* subsessile, the ovary ovoid, 1 mm long, the hypanthium 1–2 mm long, the styles 3, 2.5 mm long. *Fruits* broadly ellipsoid, 2.5 mm long and 1.5 mm wide, the beak 1.5–2 mm long, the pericarp scarious, transparent; seeds ca. 30, ovoid, 0.2 mm long.

A pantropic sea-grass, widely distributed in the Indian and Pacific oceans; in the Atlantic mainly in the Caribbean and the Gulf of Mexico, also in Brazil.

SAN BLAS: Caledonia Harbor, Mt. Vernon, *Elmore L 30* (AHFH).

2. **Halophila baillonis** Aschers. *ex* Dickie *in* Hook. f., Jour. Linn. Soc. Bot. 14: 317. 1874.—Fig. 3.

H. aschersonii Ostenf., Bot. Tidsskr. 24: 239. 1902.

Dioecious *herbs*, the rhizome thin, fragile, with 1 root at each node, the internodes 1–3.5 cm long, the scales at the base of the lateral shoots lanceolate to obovate, scarious, faintly pubescent, keeled, 1–2.5 mm long, obtuse and sometimes slightly incised apically, the margin entire; lateral shoots 6–40 mm long, erect, bearing 2 obovate scales ca. halfway up or somewhat higher, and with 2–3 pairs of leaves in an apical pseudo-whorl, the scales 3–6 mm long, often with secondary shoots arising from their axils. *Leaf-blades* oblong, ovate, or elliptic to lanceolate, rather rigid, obtuse apically, cuneate basally, the margin finely spinulose, 5–22 mm long and 2–8 mm wide, 3–8 cross-veins ascending at angles of 60–80° on each side of the midrib, joining the intramarginal veins, the midrib uniting with the

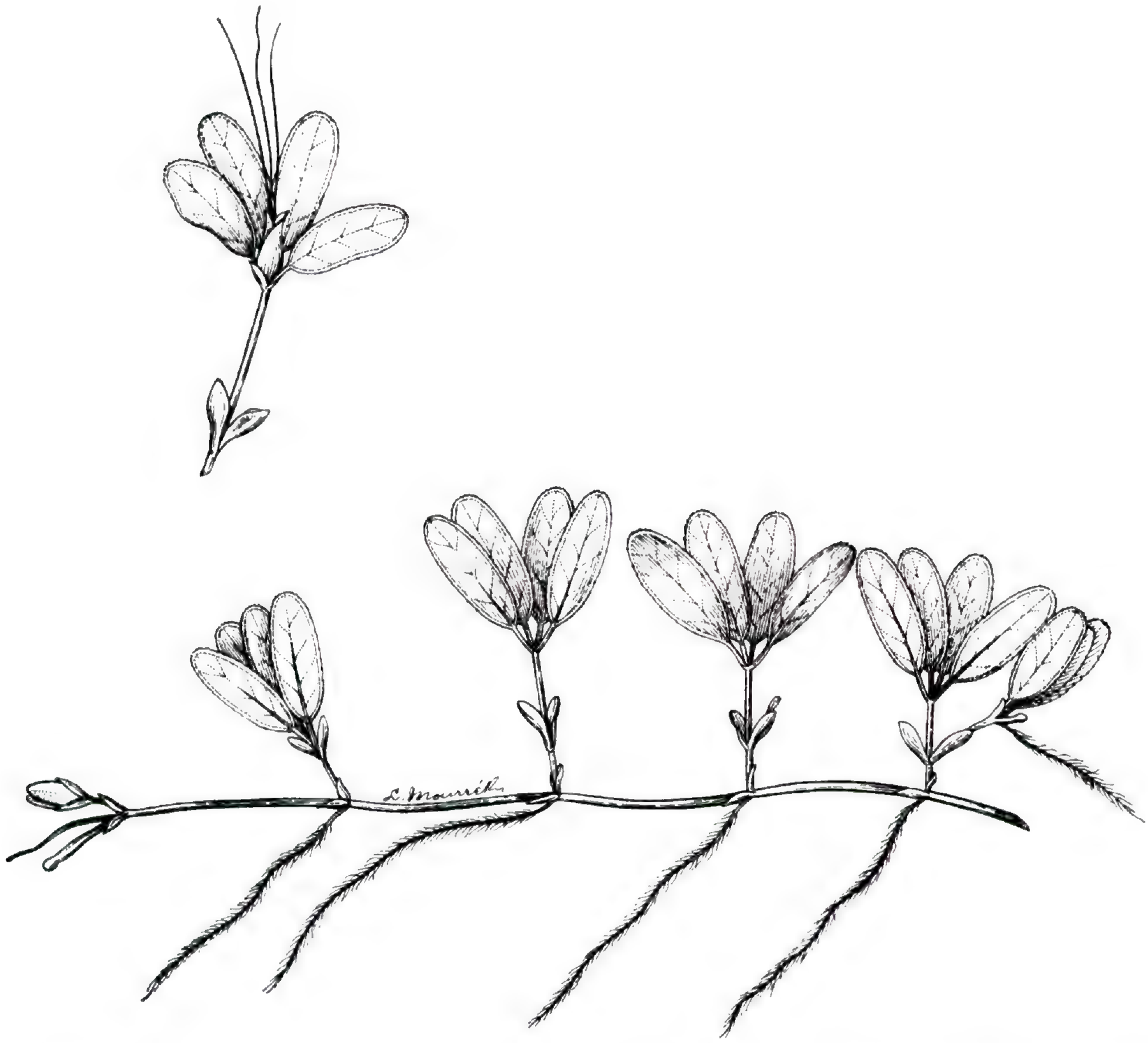

FIGURE 3. *Halophila baillonii* Aschers. *ex* Dickie *in* Hook. f. [After Ostenfeld, Bot. Tidsskr. 24: 239. 1902.]

intramarginal veins just below the apex; petioles 2–5 mm long. *Inflorescences* with the spathal leaves lanceolate, slightly unequal, acute, 5–8 mm long, somewhat enlarged after anthesis, sessile in the axil of the uppermost leaf, containing only 1 flower. *Staminate flowers* with the pedicels 3 mm long, the tepals elliptic, 4 mm long and 2 mm wide, convex, transparent with a dark stripe in the middle, apiculate, the anthers oblong, 2-thecate, 4 mm long. *Carpellate flowers* 6–7 mm long, consisting of a minute perianth and a sessile ovary gradually continuing into the hypanthium, the styles 2, 3, or 5, 10–30 mm long, with conspicuous papillae. *Fruits* globose, 2–3 mm in diameter, the beak 4–5 mm long, projecting between the spathal leaves after anthesis, the pericarp fleshy; seeds 10–20, subspherical, apiculate at both ends, the testa reticulate.

Widely distributed in the Caribbean, extending eastward to Pernambuco, Brazil; also along the Pacific coast of Panama.

VERAGUAS: Isla Jicarón, on a silt bottom at a depth of 3.5–5 m, along the N side of island, *Dawson 21103* (L, UC).

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IV

FAMILY 50A. RAFFLESIACEAE

ALWYN H. GENTRY[2]

Herbs parasitic on roots or branches of various woody hosts, thalloid or vegetatively reduced to a mycelium-like tissue, dioecious, monoecious or rarely with perfect flowers. *Leaves* reduced to scales. *Flowers* very small to exceedingly large, usually solitary, rarely spicate, subtended by bracts; calyx more or less epigynous, sometimes petaloid, composed of 4–10 distinct or basally connate segments; corolla absent; stamen number indefinite, in 1–3 series around a fleshy stylar column, the anthers sessile, dehiscing by slits or terminal pores; pollen often viscous; ovary inferior to subinferior, unilocular with 4, 6, or 8 carpels, the placentae parietal with numerous ovules, style 1 or wanting, the stigma discoid, capitate or multi-lobate. *Fruit* fleshy, indehiscent or opening irregularly; seeds numerous, minute, with cellular endosperm and a minute embryo.

A tropical and subtropical family of 8 genera and about 50 species, mostly of the Old World. The New World genera are *Pilostyles*, ranging from South America to the southwest United States, *Apodanthes* from South America to British Honduras, *Bdallophyton* in Mexico, and *Mitrastemon* with species both in the Old World and in Mexico and Guatemala. The flowers range from minute in the Panamanian species to that of *Rafflesia arnoldii* of southeast Asia which weighs up to 10 kg and is the largest flower known.

a. Parasitic on species of Flacourtiaceae; sepals petaloid, early deciduous, conspicuously narrowed to a more or less circular base ..... 1. *Apodanthes*
aa. Parasitic on species of Leguminosae; sepals not differentiated from the bracts, usually persistent, very little narrowed to a wide linear base ..... 2. *Pilostyles*

1. APODANTHES

Apodanthes Poit., Ann. Sci. Nat. Bot., Sér. 1. 3: 422, *t. 26*. 1824. TYPE: *A. caseariae* Poit.

Minute thalloid *parasites* on branches of species of Flacourtiaceae. *Inflorescence* a solitary flower, the thickened receptacle subtended by several imbricately enclosing bracts, the lowest whorl of 2 scales, the inner whorl of 4 scales. Flower whitish, turning reddish or brownish with age, the calyx segments 4, petaloid, narrowed at the base, inserted near the top of the ovary, deciduous; anthers in 2 series around a capitate central stylar (sterile) column; ovary subinferior, 1-

[1] Assisted by National Science Foundation Grant GB-362-02X.
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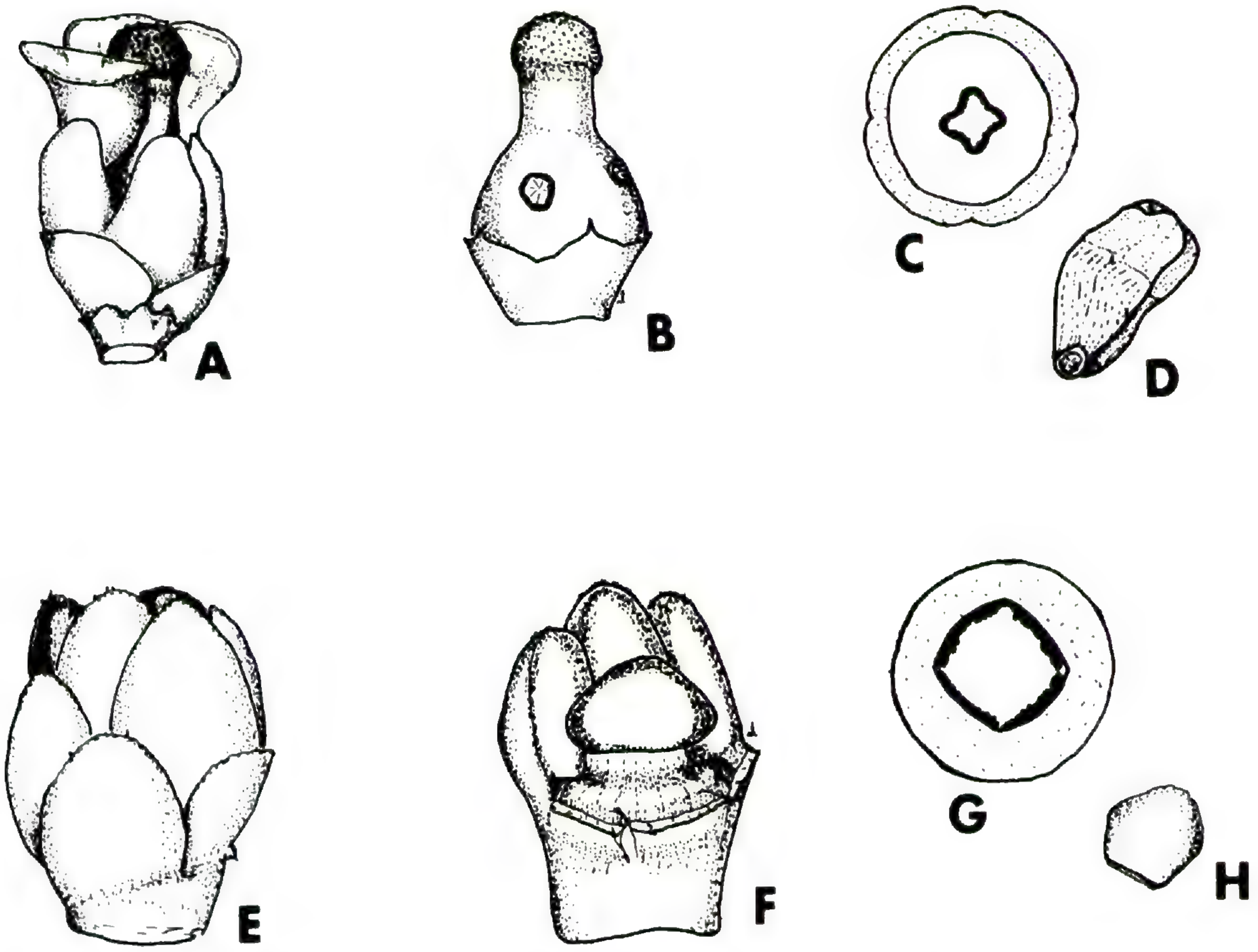

FIGURE 1. A–D. *Apodanthes casearíae* Poit.—A. Inflorescence with one tepal removed to show pistil (× 7).—B. Pistil showing insertion scar of tepal (× 8).—C. Ovary cross section (× 8).—D. Tepal (× 7). [After *Gentry 1460* (MO).]—E–H. *Pilostyles blanchetii* (Gardn.) R. Br.—E. Inflorescence (× 14).—F. Flower with bracts removed to show style and top of ovary (× 14).—G. Cross section of ovary (× 14).—H. Tepal (× 7). [After *Dressler 3380* (MO).]

celled with 4 protruding parietal placentae, the ovules numerous, the style distinct, the stigma capitate, the receptive surface apparently an annulus around the top of the stylar column at the base of the capitate enlargement. *Fruit* a berry.

Species variously interpreted as 2 to 7, all in South America with a single species reaching Panama and British Honduras.

1. **Apodanthes casearíae** Poit., Ann. Sci. Nat. Bot., Sér. 1. 3: 422. 1824. TYPE: French Guiana, *Poiteau s.n.* (not seen).

Achlorophyllous *parasites* on various species of Flacourtiaceae, the leafless plants usually numerous and arranged more or less in rows along the stem or branches of the host. *Inflorescences* 1-flowered with a fleshy, thickened receptacle subtended by ca. 6 imbricate bracts. *Flowers* 4–6 mm long, 2–3 mm wide, the calyx epigynous, of 4 petaloid, whitish, obovate segments, each narrowed to a circular base and inserted near the top of the ovary; male flowers (after Vattimo, Mus. Natl. Hist. Nat. Paris 15: 226. 1956) with a short central sterile stylar column terminating in a hemispheric stigma-like cap; stamens inserted around the stylar column below the cap in 2 series of ca. 19 anthers each, subsessile; female flowers with a single pistil, the ovary hemispherical, 3 mm long, 2.5–3 mm wide, some-

what sunken into the receptacle at the center, unilocular with 4 parietal placentae, each with numerous ovules, the style 1.5 mm long, the stigma apparently an annulus around the style apex, the apex 0.5 mm long, 1 mm wide. *Fruit* a berry, the bracts persistent, the calyx deciduous.

This species was observed as a parasite on the Barro Colorado Island populations of *Casearia stjohnii* Johnst. and *C. guianensis* (Aubl.) Urb. At the Tropic Test Center test area at Curundu, Canal Zone, it is common locally on *C. guianensis*, and it has been observed on this species in Madden Forest. The collection of *Apodanthes* from Coclé Province is apparently referable to this species, but it lacks host data.

Standley and Steyermark (Fieldiana, Bot. 24(4): 102. 1946) identified the Central American species with *Apodanthes casearíae*, although Standley earlier (Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 149. 1929; Contr. Arnold Arbor. 5: 61. 1933) had called it *A. flacourtiae* Karst. Vattimo (Rodriguésia 26: 45. 1971) considered the Panamanian plant a new species with *Woodson & Schery 965* as its type. The minor differences in tepal shape used to separate the species of this complex have been overemphasized as is manifested in differing descriptions of the petals of the same plant by different botanists. For example, the petals of the type of *A. casearíae* were described by Poiteau as cordate with an appendiculate base, by Hooker (*in* DC., Prodr. 17: 110–116. 1873) and by Solms-Laubach (*in* Mart., Fl. Bras. 4(2): 18–126. 1878) as rounded-obovate. Vattimo (*loc. cit.*) would segregate the Panamanian material on the basis of the ovate-orbicular rather than cordate petals, but these petals match the descriptions of both Hooker and Solms-Laubach for *A. casearíae*. Vattimo's earlier, 1956 opinion that *A. flacourtiae* and *A. casearíae* may be the same seems more acceptable. Some of the other names proposed by Vattimo may also prove to be synonyms of *A. casearíae*.

CANAL ZONE: Parasitic on *Casearia stjohnii*, Chapman Cove, Barro Colorado Island, *Croat 17021* (MO). Parasitic on *Casearia stjohnii*, Thomas Barbour Trail 100, Barro Colorado Island, *Croat 17044* (MO). Stem parasite on *Xylosma* [*Casearia stjohnii*], flowers visited by small butterflies and mosquitoes, Shannon end near shoreline, Barro Colorado Island, *Foster 1226* (MO). Parasitic on *Casearia guianensis*, Curundu, *Gentry 1460, 1470* (both MO). Parasitic on *Casearia stjohnii*, Barbour 2, Barro Colorado Island, *Gentry 1733* (MO). On *Xylosma* [*Casearia*] edge of plantation, Barro Colorado Island, *Wilson 139* (MO). Parasite on tree, Barro Colorado Island, *Woodson & Schery 965* (MO). COCLÉ: Near El Valle in mountain forest, *Bartlett & Lasser 16696* (MO).

2. PILOSTYLES

Pilostyles Guill., Ann. Sci. Nat. Bot., Sér. 2. 2: 21. 1834. TYPE: *P. berteri* Guill.

Frostia Bertero *ex* Guill., Ann. Sci. Nat. Bot., Sér. 2. 2: 19. 1834, *nomen nudum.*
Sarna Karst., Linnaea 28: 414. 1856. TYPE: *S. ingae* Karst. (female) or *S. caulotreti* Karst. (male).

Minute thalloid *parasites* on stems and branches of species of Leguminosae (*Bauhinia* in Panama), the plants usually numerous. *Inflorescence* 1-flowered, the thickened receptacle subtended by a number of more or less spirally arranged, imbricate bracts, the upper bracts not narrowed at the base and not differentiated as a distinct whorl of tepals. *Flowers* minute, described as purple or reddish;

anthers 2-seriate around a capitate central stylar column; ovary inferior, 1-celled, with unevenly and usually indistinctly separated peripheral parietal placentae, the ovules numerous, the style distinct, capitate, the stigmatic surface apparently an annular ring around the apex of the stylar column below the capitate enlargement. *Fruit* a berry.

About a dozen species (19 according to Vattimo, Rodriguésia 26: 45. 1971), mostly in Central and South America but one in Persia and one in Australia; two African species usually included in this genus were separated by Vattimo as *Berlinianche*. One species reaches the extreme southwestern United States.

1. **Pilostyles blanchetii** (Gardn.) R. Br., Trans. Linn. Soc. London, Bot. 19: 247. 1844.

Apodanthes blanchetii Gardn. *in* Hook., Icones Pl. *t. 655B*. 1844. TYPE: Brazil, Bahia, *Blanchet 2861* (MO).
Frostia blanchetii (Gardn.) Karst., Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 26: 922. 1858.
Sarna caulotreti Karst., Linnaea 28: 415. 1856. TYPE: Venezuela, *Karsten s.n.* (not seen).
Apodanthes globosa S. Wats. *ex* Robins., Bot. Gaz. (Crawfordsville) 16: 84. 1911. Type: Mexico, Nuevo León, Pringle *s.n.* (not seen).
Pilostyles globosa (S. Wats. *ex* Robins.) Solms-Laubach *in* Engl., Pflanzenreich 4. 75: 14. 1901.

Achlorophyllous *parasites* on various species of *Bauhinia*, the plants usually numerous and arranged in irregular rows along stems of the host. *Inflorescence* 1-flowered. *Flowers* 2–3 mm long, 2–3 mm wide, the fleshy receptacle subtended by a number of imbricate bracts, the bracts more or less obovate, the uppermost not differentiated into petaloid tepals, 1.5–2 mm long, 1–2 mm wide at base, inserted near top of the ovary; male flowers (*Blanchet 2861*) with a central stylar column terminating in a hemispheric, papillose cap, the basal row of papillae enlarged; anthers in a 2-seriate ring below the stylar cap; female flowers with a single pistil, the ovary inferior, subspherical, 2–3 mm diameter, unilocular with 2 or 4 irregular and poorly demarcated peripheral, parietal placentae, these sometimes more or less meeting and the whole inner surface of the ovary appearing placentiferous, the ovules numerous, the style 0.5 mm long, its capitate apex 1 mm long and 1.5 mm wide, the stigma annular around the base of the style apex. *Fruit* a berry.

This species is parasitic on *Bauhinia guianensis* Aubl. in Panama. It has been collected only once and is apparently rare.

The Panamanian plant is assigned to *Pilostyles blanchetii* with reservation. It differs from the female flowers of that species illustrated by Gardner in its tendency toward irregularly separated placentae and in its distinctly narrowed style. The isotype of *P. blanchetii* at Missouri Botanical Garden appears to have only male flowers, so characteristics of the style have not been checked directly. However, Vattimo (*loc. cit.*), after examining fragments of the Kew holotype, keys *P. blanchetii* out as having a distinct style. Also, the male flowers of the type collection are similar to those of some other species which have distinct styles in the female flowers. Possibly the plant figured by Gardner is in young fruit which could account for the thickening of its style.

Placentation likewise appears to provide relatively minor characters for sepa-

rating the three species of *Pilostyles* parasitic on *Bauhinia*. *Pilostyles globosa* (*ex descr.*) supposedly has the ovules distributed in small, isolated groups over the entire inner surface of the ovary; *P. caulotreti* (according to Vattimo's key) has the ovules on 4 distinct placentae; and *P. blanchetii* (from Gardner) has them distributed evenly over the entire inner surface. Mature female flowers of *P. globosa* (*Pringle 2679* (MO)) which I dissected had larger placental areas than described for the type, and these were more or less separated into four indistinct placentae. The Panamanian collection had two slightly and irregularly separated placental areas, these sometimes with a hint of further subdivision into four placentae. The placentation of this collection appears to be intermediate between that of *P. globosa* and *P. caulotreti* on the one hand and *P. blanchetii* on the other hand.

Pilostyles globosa, described from Mexico and also parasitic on *Bauhinia*, was separated in Vattimo's key on the basis of its smaller flowers, but the type specimen was clearly noted as being in bud, and a later collection (*Pringle 2679* (MO)) by the same collector from the same locality includes flowers 2–3 mm long. The tepal margins of this collection are irregularly fimbriate-ciliate as in the type material of *P. blanchetii* and as described for *P. caulotreti*, and cannot be used to support species segregation. Vattimo (Notul. Syst. (Paris) 15: 226. 1956) also noted the inconsistency of ciliate bract and tepal margins in *P. calliandrae*.

Hooker (*in* DC., Prodr. 17: 116. 1873) speculated that *Pilostyles caulotreti*, known to him from male flowers only, might represent the masculine flowers of *P. blanchetii*. The discovery of the genus in Panama closes one of its largest disjunctions and further supports Hooker's view that the plants parasitic on *Bauhinia* might all be referable to the same species. This agrees with a general pattern which seems to be emerging for this group: wide-ranging species with each host genus parasitized by only one of them. (Note also the case of *Apodanthes casearíae* discussed above and Vattimo's (1956) union of *P. mexicana* (Brandeg.) Rose with *P. calliandrae* (Gardn.) R. Br.)

PANAMÁ: Region of Cerro Jefe, flowers purple, parasitic on stem of *Bauhinia*, *Dressler 3380* (MO, PMA).

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Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 90. SIMAROUBACEAE[1]

DUNCAN M. PORTER[2]

Trees or shrubs, rarely suffrutescent, all parts often bitter to the taste. *Leaves* usually alternate, pinnately-compound, simple, or rarely rudimentary, never punctate-glandular, the margins usually entire; stipules usually absent. *Inflorescences* terminal and/or axillary or rarely cauliflorous, usually many-flowered, panicles or racemes, the flowers rarely solitary; plants monoecious or dioecious. *Flowers* small or large, regular, hypogynous, 3–5(–8)-merous, bisexual or unisexual by abortion; sepals 3–8, free or connate, imbricate or valvate, deciduous or persistent; petals 3–8, rarely absent, free, imbricate or valvate; stamens as many or twice as many as the petals, rarely more numerous, absent or reduced to staminodes in carpellate flowers, the filaments free, sometimes appendaged basally, usually inserted at the base of the disc, the anthers 2–4-thecate at anthesis, versatile or basifixed, introrse, longitudinally dehiscent; disc usually present, intrastaminal; gynoecium 2–5(–8)-carpelled, apocarpous or syncarpous, inserted on or encircled by the disc, sessile or on a gynophore, rudimentary or absent in staminate flowers, the ovaries 1-carpelled and -loculed in apocarpous flowers, 2–4-carpelled and -loculed in syncarpous flowers, the ovules 1–2 per locule, rarely more, anatropous or rarely orthotropous to campylotropous, epitropous to rarely apotropous, pendulous, placentation axile, the styles apical, lateral, or basal, free or partially to completely coherent or connate, the stigmas simple. *Fruits* apocarpous and of 2–8 1-carpelled and -loculed drupes, berries, or samaras, or syncarpous and of 2–4-carpelled and 1–4-loculed berries, drupes, samaroid capsules, or schizocarps; seeds 1 per locule, the testa membranaceous or coriaceous, the endosperm absent or scanty, the embryo large and straight or rarely curved, the cotyledons narrow, mostly fleshy, plano-convex or flat, the radicle usually short.

A family of about 30 genera and 200 species, mainly tropical except for a few species in warm-temperate eastern Asia and western North America. Four genera are known to occur in Panama. The bitter vegetative parts of many species are used medicinally.

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[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

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ANN. MISSOURI BOT. GARD. 60: 23–39. 1973.

Useful references:

Cronquist, A. Studies in the Simaroubaceae—IV. Resumé of the American genera. Brittonia 5: 128–147. 1944.

Brizicky, G. K. The genera of Simaroubaceae and Burseraceae in the Southeastern United States. Jour. Arnold Arbor. 43: 173–186. 1962.

a. Leaf petiole and rachis broadly and conspicuously winged ..... 1. *Quassia*
aa. Leaf petiole and rachis not winged.
  b. Leaflets 20–36, opposite to the lower most pairs subopposite, tipped with a conspicuous apical gland ..... 2. *Simaba*
  bb. Leaflets 3–20, alternate to the lowermost pairs subopposite or opposite, not tipped with a conspicuous apical gland.
    c. Inflorescences widely-branching panicles; stamens or staminodes 10; drupes 1–3 per flower, 1-seeded ..... 3. *Simarouba*
    cc. Inflorescences simple spike-like racemes, rarely once-branched basally; stamens or staminodes 3–5, or absent; berries 1 per flower, 1–3-seeded ..... 4. *Picramnia*

1. QUASSIA

Quassia L., Sp. Pl., ed. 2. 553. 1762; Gen. Pl., ed. 6. 212. 1764.

Shrubs or small trees, all parts quite bitter to the taste. *Leaves* alternate, odd-pinnate; petiole and rachis conspicuously winged and articulated; leaflets 5–7, opposite, entire, sessile. *Inflorescences* axillary or rarely terminal or cauliflorous, racemose or rarely paniculate basally. *Flowers* large, 5-merous, bisexual, the pedicels articulated below the apex; sepals 5, free, imbricate; petals 5, pink or red, free, contorted, not spreading at anthesis; stamens 10, exerted, the filaments filiform, appendaged basally, the anthers versatile; intrastaminal disc conspicuous, enlarging in fruit; gynoecium 5-carpelled, apocarpous, but the styles connate, the ovules 1 per locule, pendulous, anatropous, placentation axile, the stigma simple or slightly lobed. *Fruit* a drupe, 1–5 per flower, oblong, ridged, the mesocarp thin, the endocarp crustaceous; seeds 1.

Monotypic. Nooteboom (Blumea 11: 509–528. 1962) has treated *Quassia* in an extremely broad sense, subordinating several genera (including *Simaba* Aubl. and *Simarouba* Aubl.) best considered separately. His treatment is quite artificial and has little to recommend it.

1. **Quassia amara** L., Sp. Pl., ed. 2. 553. 1762.—FIG. 1.

Q. officinalis L. Rich., Actes Soc. Hist. Nat. Paris 1: 108. 1792.
Q. alatifolia Stokes, Bot. Mat. Med. 2: 491. 1812.
Q. amara var. *paniculata* Engl. *in* Mart., Fl. Bras. 12(2): 207. 1874.
Q. amara var. *grandiflora* Hemsl., Biol. Centrali-Amer. 1: 172. 1879. *nom. und.*
Q. amara fo. *paniculata* (Engl.) Cronquist, Brittonia 5: 146. 1944.

Slender *shrubs or small trees*, 2–8 m high, the bark exfoliating in small flakes; branchlets reddish, angled. *Leaves* odd-pinnate, 21–31 cm long and 9–24 cm wide; petiole and rachis oblanceolate-winged, the wing to 15 mm wide apically, rarely also slightly auriculate; leaflets (3–)5(–7), opposite, obovate to oblanceolate, abruptly acuminate apically, cuneate basally, chartaceous, sessile, 4–22.5 cm long and 16–75 mm wide, the terminal usually largest. *Racemes* axillary or sometimes terminal or rarely cauliflorous, rarely paniculate basally, the branches red, mi-

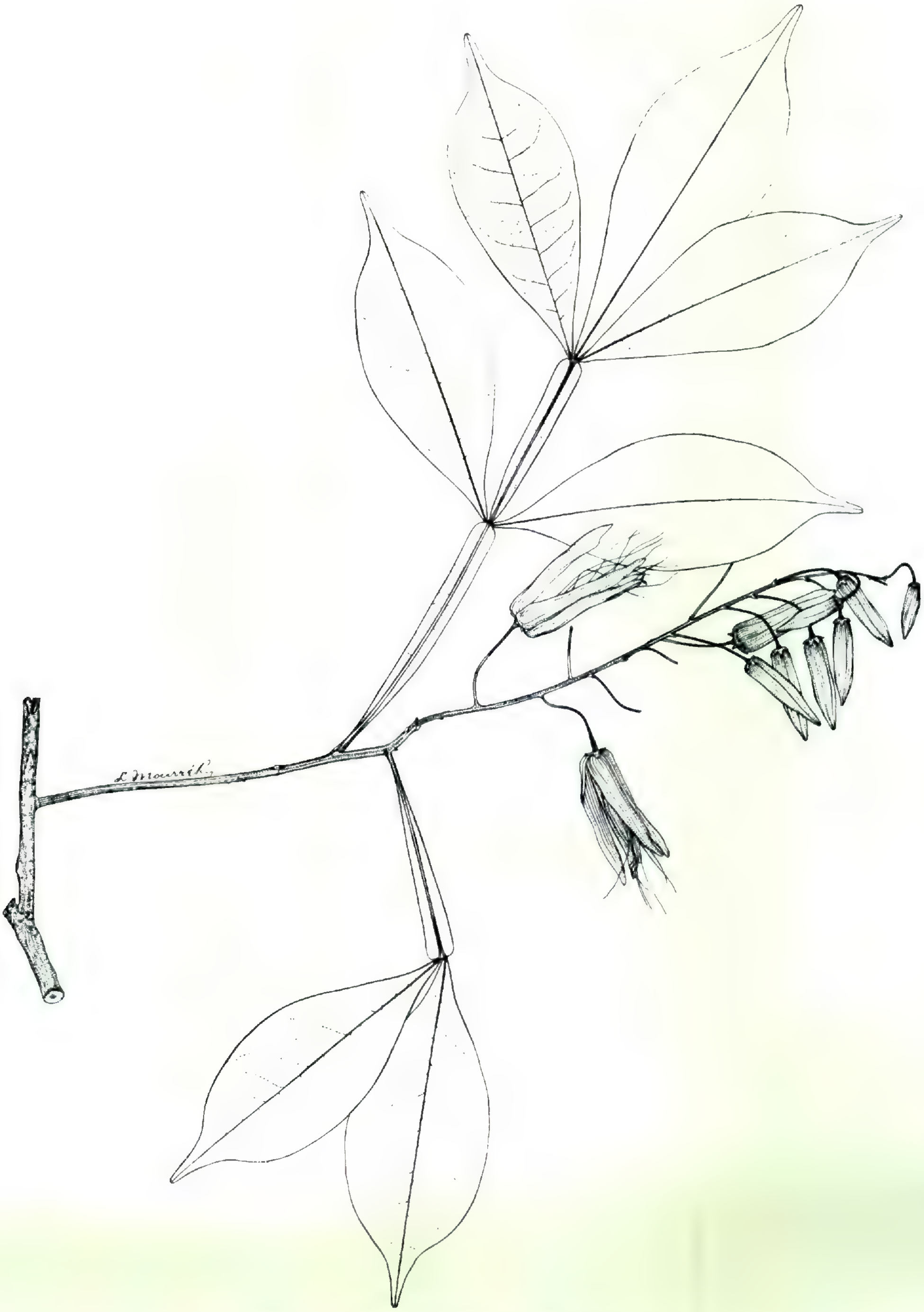

FIGURE 1. *Quassia amara* L., habit (× 5/12).

nutely puberulent, 6.5–28 cm long. *Flowers* showy, the buds conical, the pedicels red, minutely puberulent, articulate below the apex, 5–30 mm long, subtended by a pubescent lanceolate bract ca. 2 mm long; sepals 5, pink to red, triangular, ciliate, ca. 1.5 mm long and wide; petals 5, pink to bright red, white within,

lanceolate, pubescent basally within, 3–4 cm long and 5–6 mm wide, not spreading at anthesis; stamens 10, exserted, 3.5–4 cm long, the filaments filiform, appendaged basally, the appendages pubescent, coherent; intrastaminal disc conspicuous, 10-lobed, enlarging and becoming red in fruit; carpels 5, ovoid, free below, but connate above to form the style, the style as long as or longer than the stamens, to 5 cm long, deciduous, the stigma simple or slightly lobed. *Drupes* 1–5 per flower, oblong, stalked, with a medial ridge, veined, glabrous, green to reddish, becoming dark red at maturity, ca. 15 mm long and 8 mm wide, forming a star-shaped cluster spreading from the broad red disc.

Native to tropical America, occurring from Brazil to Mexico and the West Indies and occasionally naturalized in the Old World tropics. *Quassia amara* has been widely cultivated in the American tropics for its medicinal properties, and its original range is impossible to determine.

In Panama known to flower in all months but April, May, and July, with the peak period from October to January. Known to fruit in all months save from July through September, with the peak apparently in December and January.

BOCAS DEL TORO: Water Valley, *von Wedel 1429* (GH, MO, US), *1477* (GH, MO, US), *1691* (MO), *1700* (GH, MO, US), *1844* (GH, MO, NY, US), *2151* (MO). CANAL ZONE: Barro Colorado Island, *Brown 145* (F), *Dwyer et al. 8462* (MO), *Frost 80, 138* (both F), *Hunnewell 16438* (GH), *Oppenheimer 67-1-9-1316* (MO), *Sharp*, 1962 (SCZ); moist woods, *Standley 31302* (A, US), wet forest, *41030* (A, US); back of lab, *Aviles 69* (F, MO); lake shore N of dock, *Croat 4754, 7111* (both MO); Barbour-Lathrop Trail, *Shattuck 51* (A, F, MO); Barbour-Van Tyne Trail, between station and Big Tree, *Graham 198* (GH); shoreline S of Colorado Point, *Croat 6144* (MO); shore, Drayton Inlet, *Foster 1312* (DUKE); Fairchild Trail 100, *Croat 4005A* (MO, NY, SCZ), ca. 500, *Wetmore & Abbe 5A* (A, F, GH, MO); Lake Trail 500, *Croat 6279* (MO); Lathrop Trail 5.5, *Hladik 12* (MO); Nemesia Trail 400, *Croat 8591* (MO); Snyder-Molino Trail, *Croat 4038* (MO), *Ebinger 25* (MO, US), *Killip 39965* (US); Wheeler Trail, *Weaver & Foster 1570* (DUKE), 500, *Wetmore & Abbe 5* (A, F, GH, MO). Chagres, *Fendler 304* (F, MO, US). Near Coco Solo weather station, *Duke 4275* (MO). 5 mi. NW of Cocolí, 500 ft, *Tyson 1615* (MO, SCZ). Near Coro Solito Naval Hospital, *Harvey 5024* (F). Near Fort Randolph, brushy slope, *Standley 28694* (US). Fort Sherman, road to San Lorenzo, *Quistgaard 82* (MO). Between France Field and Cativa1, Colón, brushy slope, *Standley 30337* (A, MO, US), wooded swamp, *30453* (US). Vicinity of Frijoles, *Piper 5795, 5803, 5833* (all US). Hills N of Frijoles, wet forest, *Standley 27417* (US). Gatun, woods along railroad, *Pittier 2562* (US). Between Gatun and Lion Hill, 10–20 m, *Pittier 2562* (F, GH, MO, NY). Hills off Road K-15 near Huile, secondary and cut-over primary forest, *Smith et al. 3280* (F, GH). Lion Hill Station, *Hayes 116* (NY), *159* (GH, US). Pipeline Road, *Haines & Correa A. 533* (A, MO), *Sharp*, 1962 (SCZ), ca. 15 mi. from Gamboa, *Blum 2044* (MO, SCZ), ca. 16 mi. NW of Gamboa at end of trail along forest edge, *Wilbur & Teeri 13399* (DUKE). Río Indio, drowned forest, 66 m, *Steyermark & Allen 16775* (MO). Santa Rita Trail, *Cowell 133* (NY). Summit, *Lindsay 231* (MO, SCZ). Taboga Island, dense thicket, *Macbride 2803* (F, MO, US), along stream in forest, *Welch 19851* (MO). COCLÉ: Road to El Cope from InterAmerican Highway, *Burch et al. 1375* (F, MO, NY). COLÓN: Tres Brazos sawmill, Icacal, *Howell 8* (MO). DARIÉN: Without locality, *Bristan 181* (MO), *Sexton 114* (MO). Near El Punteadero, InterAmerican Highway bridge shortly downstream on Río Chucunaque from Yaviza, deep woods on rocky ridge, *Stern et al. 169* (GH, MO, US). Vicinity of El Real, *Allen 942* (GH, MO, NY, US); 2–3 mi. SE of El Real, *Duke 4840* (MO). Near Refugio, 15–21 mi. N of Santa Fé, ca. 30 m, *Duke 10306* (MO). Río Chico, secondary forest in swamps and hillsides, *Burch et al. 1102* (MO, US). Río Paya, *Duke & Kirkbride 14074* (MO). PANAMÁ: Between Cañasas and Sabalo, ca. 100 m, *Duke 14471* (MO). Near Chepo, *Kluge 36* (F, US). Quebrada Ancha, *Steyermark 16775A* (MO). Tributary of Río Chagres 5 mi. SW of Cerro Brewster, shady and rocky river banks, ca. 1000 ft, *Lewis et al. 3383* (MO, SCZ). Sabanas, N of Panama City, *Bro. Paul 620* (US). VERAGUAS: Vicinity of Santa Fé, forming thickets along rivers under larger trees, 1000 ft, *Allen 4438* (MO).

This species occurs at low elevations in areas of monsoon forest and evergreen seasonal forest. Common names reported are "crucete" (fide *Sharp*, 1962; *Standley 27417*), "guabo amargo" (fide *Howell 8*), "guavita amarga" (fide *Sharp*, 1962), "guavito" (fide *Kluge 36*, *Sexton 114*), "hombre grande" (fide *Duke & Kirkbride 14074*), "juavita amarga" (fide *Smith et al. 3280*), and "udut pulu" (fide *Duke 14471*).

Some of the uses of *Quassia amara* have been listed by Standley (Contr. U. S. Natl. Herb. 27: 223. 1928): "All parts of the plant are as bitter as quinine, this flavor resulting from a principle, quasin, which was formerly believed to be of value as a febrifuge. At present an infusion of the wood in alcohol is used in parts of Panama as a remedy for fevers. The plant furnishes the bitterwood or quassia of commerce, which is employed in the manufacture of insecticides, as a substitute for hops in ale and beer, and in the preparation of propietary medicines and 'conditioning powders' for domestic animals. . . . It is said to be used in Panama as a remedy for snake bites." The Bayano Cuna Indians of eastern Panamá Province cultivate *Q. amara* as a medicinal plant (fide *Duke 14471*).

2. SIMABA

Simaba Aubl., Hist. Pl. Guiane Fr. 1: 400. 1775.

Aruba Aubl., op. cit. 1: 293. 1775.
Zwingera Schreb., Gen. Pl. 2: 802. 1791.
Homalolepis Turcz., Bull. Soc. Imp. Naturalistes Moscou 21(1): 575. 1848.
Odyendyea (Pierre) Engl., Nat. Pflanzenfam. 3(4): 215. 1896.

Trees or shrubs, rarely suffrutescent and the leaves all basal, all parts quite bitter to the taste. *Leaves* alternate, usually even-pinnate, sometimes only the terminal leaflet present and the leaf appearing simple; leaflets (1–)4–40, usually opposite, entire, petioluled to sessile. *Inflorescences* usually large terminal or axillary panicles, sometimes reduced to axillary, few-flowered, umbel-like clusters or to umbel-like panicles. *Flowers* small to large, 4–5-merous, bisexual; sepals 4–5, connate at least basally, imbricate; petals 4–5, free, pubescent, imbricate, more or less spreading at anthesis; stamens 8–10, appendaged basally, the filament adnate to the pubescent appendage only basally to throughout its length; intrastaminal disc conspicuous, elongating in fruit; gynoecium 4–5-carpelled, the carpels sessile on the disc, 1-loculed, cohering or weakly connate axially to form a deeply 4–5-lobed ovary, the ovules 1 per locule, pendulous, placentation axile, the style 1, the stigma capitate to slightly lobed. *Fruit* a drupe, 1–5 per flower; seeds 1.

Perhaps 30 species, most in tropical America, but a few in tropical Africa. Nooteboom (Blumea 11: 518–524. 1962) reduced the genus to a section of *Quassia*, recognizing 32 species, including one from Malaysia and two from Australia. *Quassia* and *Simaba* certainly are closely related, but they are best considered separate genera.

Useful reference:

Cronquist, A. Studies in the Simaroubaceae. III. The genus *Simaba*. Lloydia 7: 81–92. 1944.

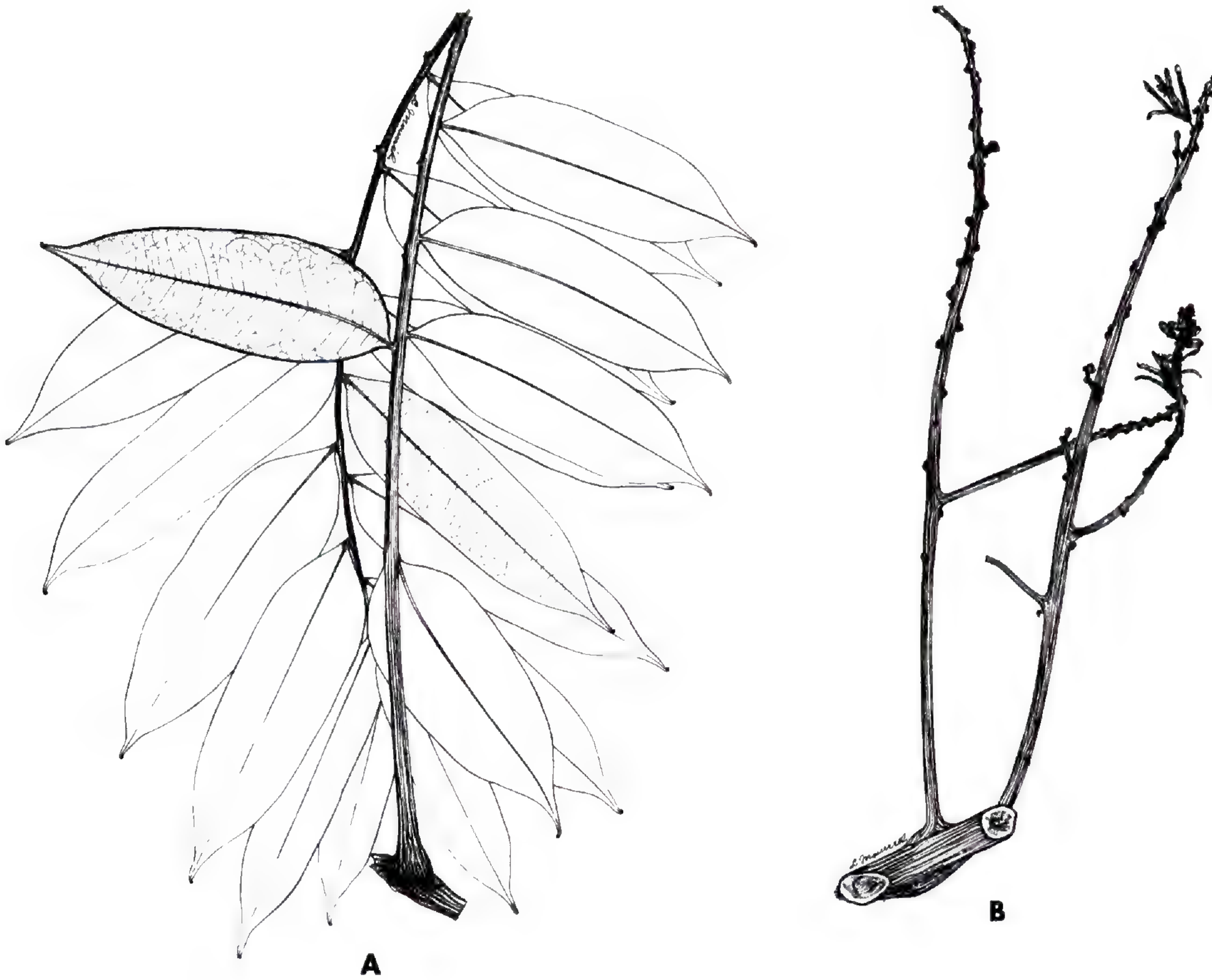

FIGURE 2. *Simaba cedron* Planch.—A. Leaf (× ¼).—B. Inflorescence (× ¼).

1. **Simaba cedron** Planch., London Jour. Bot. 5: 566. 1846.—FIG. 2.

Aruba cedron (Planch.) O. Ktze., Rev. Gen. Pl. 1: 103. 1891.

Shrubs or trees, 2–6 m high; trunk unbranched, terminated by a cluster of large leaves. *Leaves* even-pinnate, 1–2 m long; petiole and rachis minutely puberulent; leaflets 20–36, opposite to the lowermost subopposite, oblong to oblong-lanceolate, abruptly acuminate and tipped with a conspicuous indurated brownish subglobose gland apically, inequilateral and broadly cuneate basally, subsessile, the margin entire and retuse, subcoriaceous, minutely puberulent above on the veins and occasionally sparsely so beneath, the middle pairs largest, 18–25 cm long and 43–70 mm wide, the lowermost pairs smallest. *Panicles* terminal, widely-branched, spreading, brownish-tomentulose, 1–2 m long. *Flowers* with the pedicels brownish-tomentulose, 2–3 mm long; calyx brownish-tomentulose, shallowly 5-lobed, ca. 2 mm high; petals 5, greenish, free, lanceolate, thick, canescent, recurved, the margins involute, 2–3 cm long and ca. 2 mm wide; stamens 10, the filaments a little longer than the appendages, 17–19 mm long, free only in their uppermost 3–4 mm, the appendages linear-lanceolate, whitish, villous, connivent by their trichomes, adnate to the filaments for most of their length, 16–18 mm long, the anthers versatile; disc columnar, 5-lobed, 3 mm high, elongating in fruit to 5–6 mm; ovary globose, deeply 5-lobed, ca. 1 mm high, the carpels sessile,

connivent, brownish-tomentose, the style subulate, pubescent basally, equalling the stamens, 8–15 mm high, the stigma slightly clavate. *Drupes* 1 per flower, obovoid, brownish-tomentulose, reddish-brown maturing yellow, to 6.5 cm long and 4 mm wide; seed not filling the fruit cavity.

According to Cronquist, native to the Amazon basin, and now widely cultivated in Brazil, northern South America, and Central America. In Panama known to flower in March and April, and to fruit from March through July.

DARIÉN: Without locality, *Duke* 8322 (MO). 2–3 mi. SE of El Real, *Duke 4862* (MO). Trail between Paya and Payita, *Stern et al. 174* (GH, MO, US). Forests around Pinogana, *Pittier 6549* (GH, NY, US). PANAMÁ: Isla San José, open scrub, near Naval Cove, *Erlanson 410* (GH, US), thicket, road to Naval Cove, *Johnston 561* (GH, MO, US).

Commonly known as "cedrón" (fide *Duke* 8322), *Simaba cedron* is easily recognized by its palm-like habit and large leaves and inflorescences. The fruits are "used for snake bite and malaria and for stomach ache" (fide *Duke* 8322).

3. SIMAROUBA

Simarouba Aubl., Hist. Pl. Guiane Fr. 2: 859. 1775. *nom. cons.*
Simarouba Boehmer *in* Ludwig, Def. Gen. Pl. 513. 1760.

Trees or shrubs, the bark and wood bitter. *Leaves* alternate, even- or odd-pinnate, persistent; leaflets (3–)8–16(–21), alternate or rarely opposite, entire, more or less coriaceous, shortly petiolulate. *Inflorescences* large, complex, terminal and axillary panicles. *Flowers* small (4–)5(–6)-merous, unisexual, the plants dioecious; sepals (4–)5(–6), connate at least basally, imbricate; petals (4–)5(–6), green or whitish to yellow, much longer than the sepals, imbricate; stamens (8–)10(–12), ca. as long as the petals, rudimentary or absent in carpellate flowers, the filaments subulate, with an adaxial pubescent appendage basally, the anthers oblong to sagittate, versatile; intrastaminal disc more or less cushion-shaped, reduced in staminate flowers, enlarging in fruit; gynoecium (4–)5(–6)-carpelled, rudimentary or absent in staminate flowers, the carpels sessile on the disc, 1-loculed, cohering or weakly connate axially to form a deeply (4–)5(–6)-lobed ovary, soon separating following pollination, the ovules 1 per locule, pendulous, anatropous and epitropous, placentation axile, the styles connate into a short column, the stigmas (4–)5(–6), slender and divergent in carpellate flowers, short and lobed in bisexual flowers, and absent from staminate flowers. *Fruit* a drupe, 1–5 per flower, ellipsoid to obovoid, slightly compressed laterally, usually ridged, the mesocarp thin, the endocarp crustaceous; seeds 1, the testa thin and membranaceous, the endosperm absent, the embryo straight, the cotyledons plano-convex and fleshy, the radicle short and superior.

About six species in tropical America. Nooteboom (Blumea 11: 525–526. 1962) reduced the genus to a section of *Quassia*, recognizing four species. There is no question that *Quassia* and *Simarouba* are closely related. However, there is little justification to consider them as members of the same genus.

The bitter bark and the oily seeds of several species, including that found in Panama, have medicinal properties.

Useful reference:

Cronquist, A. Studies in the Simaroubaceae. II. The genus *Simarouba*. Bull. Torrey Bot. Club 71: 226–234. 1944.

1. **Simarouba amara** Aubl., Hist. Pl. Guiane Fr. 2: 860. 1775.—FIG. 3.

Quassia simarouba L. f., Suppl. 234. 1781.
Zwingera amara (Aubl.) Willd., Sp. Pl. 2: 569. 1799.
Simarouba amara var. *opaca* Engl., Nat. Pflanzenfam. 3(4): 213. 1896.
S. opaca (Engl.) Radlk. *ex* Engl., op. cit., ed. 2. 19a: 374. 1931.
S. amara var. *typica* Cronquist, Bull. Torrey Bot Club 71: 229. 1944.

Trees, 5–35 m high; branchlets reddish, glabrate. *Leaves* even- or odd-pinnate, to ca. 60 cm long; petiole and rachis reddish, minutely puberulent above in the sulcus, the petioles 4–7 cm long; leaflets 9–16, alternate to rarely subopposite, oblong to narrowly obovate or elliptic, rounded and abruptly short-acuminate to occasionally retuse apically, inequilateral and cuneate basally, the margin entire and retuse, thick, coriaceous, dark green and lustrous above, paler and duller beneath, the midrib impressed above, prominent beneath, the lateral veins obscure, 2.5–11 cm long and 12–45 mm wide, the lowermost usually smaller, the petiolules 1–2 mm long, minutely puberulent above in the sulcus. *Staminate panicles* terminal, widely-branched, densely-flowered, reddish, minutely puberulent, to ca. 30 cm long. *Staminate flowers* campanulate, greenish or yellowish, subtended by deciduous spathulate bracts, the pedicels minutely puberulent, 2 mm long; calyx bowl-shaped, 5-lobed, deciduous, ca. 1 mm high, the lobes broadly triangular, ciliate; petals 5, ovate, upright and slightly spreading apically at anthesis, 4–5 mm long and to 3 mm wide; stamens 10, in 2 whorls, ca. 4 mm long, the outermost whorl slightly shorter, the filaments subulate, the appendages densely tomentose, the tomentum covering the disc and intertwining to cohere adjacent filaments; the disc ca. 1 mm high, 5-lobed; the gynoecium rudimentary. *Carpellate panicles* like the staminate, but fewer-flowered. *Carpellate flowers* like the staminate, but the pedicels to 5 mm long; petals 3–3.5 mm long; stamens reduced to 10 obovoid, beaked, pubescent staminodia 1 mm high; disc 10-lobed, less than 1 mm high, pubescent to glabrate; ovary obovoid, deeply 5-lobed, glabrous, 2 mm high, the style ca. 1 mm long, deciduous, the stigmas 5, recurved, ca. 1 mm long. *Drupes* 1–3 per flower, obovoid or ellipsoid, slightly compressed laterally, markedly contracted basally, with a medial ridge and a prominent subapical stylar scar, brownish-punctate, glabrous, green to reddish, becoming blue-black at maturity, ca. 1.5 cm long.

Brazil and Bolivia north to British Honduras and the Lesser Antilles. In Panama known to flower in March and April and to fruit from March through May.

CANAL ZONE: Barro Colorado Island, *Carpenter 42* (F); in lake, cove S of Colorado Point, *Croat 9508* (MO, SCZ); shoreline S of Colorado Point, *Croat 8749* (MO), *Foster 1666* (MO); W of Fairchild Trail 390, *Croat 8416* (MO, NY, SCZ); shoreline of Gigante Bay, SE corner of cove at end of Shannon Trail, *Croat 8441* (MO, SCZ); center cove at end of Peña Blanca Peninsula, *Croat 8368* (MO, NY, SCZ); Snyder-Molino Trail, first 200 m, *Dressler 3422* (MO), 320, *Croat 4540* (MO); Wheeler Trail, *Starry 144* (F, MO); Zetek Trail 2, *Foster 831* (DUKE, MO), 250, *Croat 14026* (MO). Forest, near Indio Tower, *Johnston 1792* (A). PANAMÁ: Near Motel Su Lin along dirt road to Cerro Campana, *Correa A. & Dressler 840* (NY, SCZ).

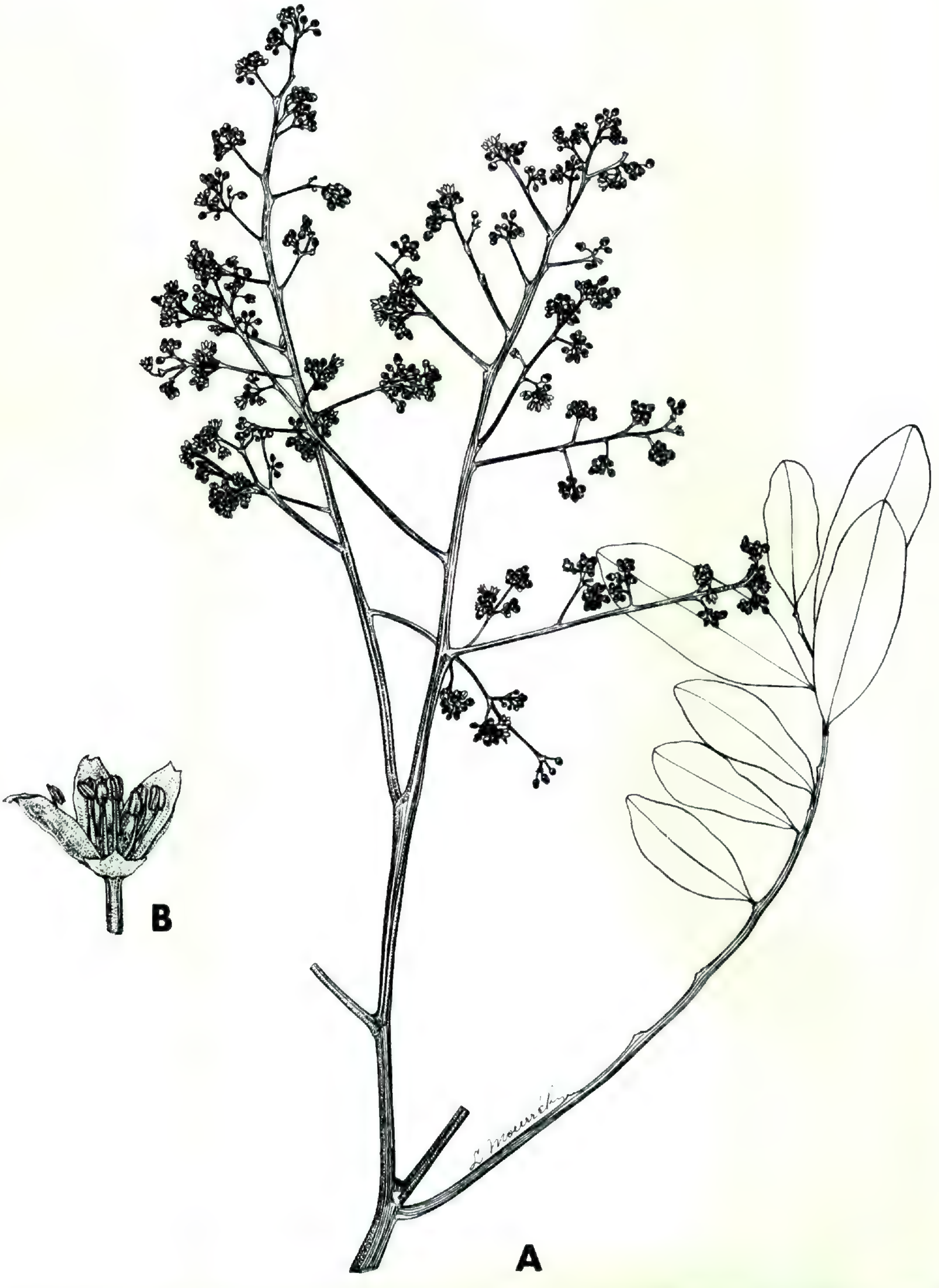

FIGURE 3. *Simarouba amara* Aubl.—A. Habit (× ½).—B. Flower (× 3¾). [After *Skutch 2510* (MO), from El General, Costa Rica.]

Simarouba amara occurs in areas of monsoon forest, evergreen seasonal forest, and premontane rain forest.

Notwithstanding Nooteboom's (Blumea 11: 525. 1962) attempt to unite *Simarouba amara* with the more northern S. *glauca* DC. under the name *Quassia simarouba* L. f., the two are amply distinct, as indicated by Cronquist (Bull. Torrey Bot. Club 71: 230. 1944). The two overlap in Costa Rica and northward, but are easily distinguished, as the flowers of S. *amara* are smaller, the calyx is conspicuously ciliate, and the petals spread only apically at anthesis.

4. PICRAMNIA

Picramnia Sw., Prodr. 27. 1788, *nom. cons.*

Pseudobrasilium Adans., Fam. 2: 341. 1763.
Tariri Aubl., Hist. Pl. Guiane Fr. 1: 37. 1775.

Shrubs or trees, usually with slender curving branches, the bark and wood often quite bitter to the taste. *Leaves* alternate, odd- or even-pinnate; leaflets (3–)6–20, alternate to opposite, usually entire, chartaceous to coriaceous, petioluled. *Inflorescences* long, slender, many-flowered racemes or panicles, aggregated to solitary, terminal to axillary. *Flowers* small, 3-, 4-, or 5-merous, unisexual, the plants dioecious; sepals 3–5, connate at least basally, imbricate; petals 3–5, or sometimes absent, linear to elliptic or lanceolate, ca. as long as or a little longer than the sepals, imbricate; stamens as many as and opposite the petals, reduced to staminodes or absent in carpellate flowers, exserted, the filaments inserted between and below the lobes of the small intrastaminal disc, rarely adnate to the petals, the anthers basifixed, 2-lobed, the lobes separated by a thick connective; gynoecium 2–3-carpelled, syncarpous, rudimentary or absent in staminate flowers, 2–3-lobed and -loculed, the ovules 2 per locule, pendulous, anatropous and epitropous, placentation axile, the style bilobed, persistent and spreading in fruit, the upper surface stigmatiferous, absent in staminate flowers. *Fruit* a berry, obovoid to ellipsoid, 1–3-loculed; seeds 1–3, 1 per locule, the testa membranaceous, the endosperm absent.

About 40 species in tropical America. This is the only New World genus of the family that was not treated by Cronquist in his series of revisions published in the 1940's, and most species are ill-defined and poorly known. Anyone attempting to identify unknown collections of *Picramnia* will surely agree with Brizicky (Jour. Arnold Arbor. 43: 182. 1962) that "The genus, which represents a subfamily of its own, is in need of a revision."

Berries of some species are eaten, while those of others are reported to have a bitter taste. Leaves, roots, and especially the bark are used medicinally.

The flowers of all species are small (less than 5 mm long) and are difficult to examine without a dissecting microscope. However, sepal number is easily determined with or without a hand lens even in fruiting specimens, as the sepals persist until the pedicels articulate and the berries drop from the plant.

a. Sepals 3.
  b. Leaflets 12–20, the secondary veins beneath glabrous ..... 1. *P. allenii*
  bb. Leaflets 7–11, the secondary veins beneath pubescent.

c. Leaflets 7–8; the blade sparingly appressed-pubescent beneath, especially basally; the lowermost leaflets acute to obtuse and inequilateral basally ..... 2. *P. cooperi*
cc. Leaflets 9–11; the blade villous beneath; the lowermost leaflets cordate basally ..... 3. *P. carpinterae*

aa. Sepals 4 or 5.
d. Sepals 4; leaflets 8–13(–17), ovate to obovate or oblanceolate, the terminal leaflets elliptic, the petiolules densely tomentose ..... 4. *P. dwyeri*
dd. Sepals 5.
e. Leaflets (3–)6–8(–9), ovate to elliptic or oblong, the petiolules sparingly pubescent to glabrate ..... 5. *P. latifolia*
ee. Leaflets 10–15, elliptic or the lowermost ovate, the petiolules densely appressed-tomentulose ..... 6. *P. corallodendron*

1. **Picramnia allenii** D. M. Porter, Jour. Arnold Arbor. 54: 315. 1973.—Fig. 4.

Shrubs or small trees, 1–7 m high; branchlets yellowish appressed-tomentulose, becoming glabrate. *Leaves* alternate, pinnate, 18–24.5 cm long; petiole and the rachis yellowish appressed-tomentulose, becoming almost glabrate; leaflets 12–20, mainly an even number, alternate to the lowermost subopposite or opposite, ovate to elliptic, narrowly acuminate apically, rounded and markedly inequilateral basally, the margins entire, revolute, chartaceous, yellowish appressed- tomentulose above and beneath on the main vein and marginally, the blade sparingly pubescent, 22–75 mm long and 8–23 mm wide, the terminal leaflets largest, the lowermost smallest and reflexed, the petiolules yellowish appressed-tomentulose, 2–3 mm long. *Staminate racemes* subterminal, becoming axillary, aggregated to solitary, simple or rarely once-branched, densely-flowered, yellowish appressed-tomentulose, to 38 cm long. *Staminate flowers* 3-merous, numerous, 1-several aggregated in clusters, white or greenish, the pedicels spreading, yellowish appressed-tomentulose, to 3 mm long; sepals 3, ovate, apiculate, appressed-pubescent, ca. 1.5 mm long and 1 mm wide; petals 3, narrowly elliptic, apiculate, glabrous to rarely sparingly pubescent, longer than the sepals, ca. 1.5 mm long; stamens 3, exserted, the filaments filiform, glabrous, ca. 2.5 mm long, ovary absent. *Carpellate racemes* solitary or in pairs, yellowish appressed-tomentulose, to 28 cm long. *Carpellate flowers* 3-merous, the pedicels appressed-tomentulose, articulated basally, 1–1.5 cm long in fruit; sepals 3, broadly triangular, appressed-pubescent, persistent and spreading in fruit, ca. 2 mm long and 1 mm wide; style bilobed, the lobes recurved and persisting in fruit. *Berries* red or orange, ellipsoid to obovoid, appressed-pubescent to glabrate, to 1.5 cm long; seeds 1.

Costa Rica and Panama. In Panama known to flower in February, May, July, and August, and to fruit in January, March, June, July, and December.

CHIRIQUÍ: Bajo Boquete, open valley, 3800 ft, *von Hagen & von Hagen 2126* (MO, NY). Bajo Lino, edge of ditch, 945 m, *Bro. Maurice 713* (US). Boquete, 3800 ft, *Davidson 616* (F, MO, US). Vicinity of Boquete, in open potrero, 1000–1300 m, *Maxon 5047* (F, NY, US), 1200–1500 m, *Woodson & Schery 738* (F, GH, MO). Boquete to 3 mi. N, second growth, cultivated areas, and roadsides, 3300–4200 ft, *Lewis et al. 635* (GH, MO). Ca. 1 mi. SW of Boquete, elevated gravel benches, 4000 ft, *Allen 4728* (F, MO). Finca Lérida to Boquete, ca. 1300–1700 m, *Woodson et al. 1140* (A, F, MO, NY). Llanos Francia, 3300 ft, *Stern et al. 1224* (MO). COCLÉ: El Valle de Antón, lower portion of valley and marshes along Río Antón, ca. 500 m, *Hunter & Allen 353* (F, GH, MO, US), along Río Indio Trail, 500–700 m, *Hunter & Allen 306* (F, MO, NY, US). Hills S of El Valle de Antón, 700 m, *Allen 2479* (US). Vicinity of El Valle, 800–1000 m, *Allen 90* (MO), in mountain forest, *Bartlett & Lasser 16666* (MO).

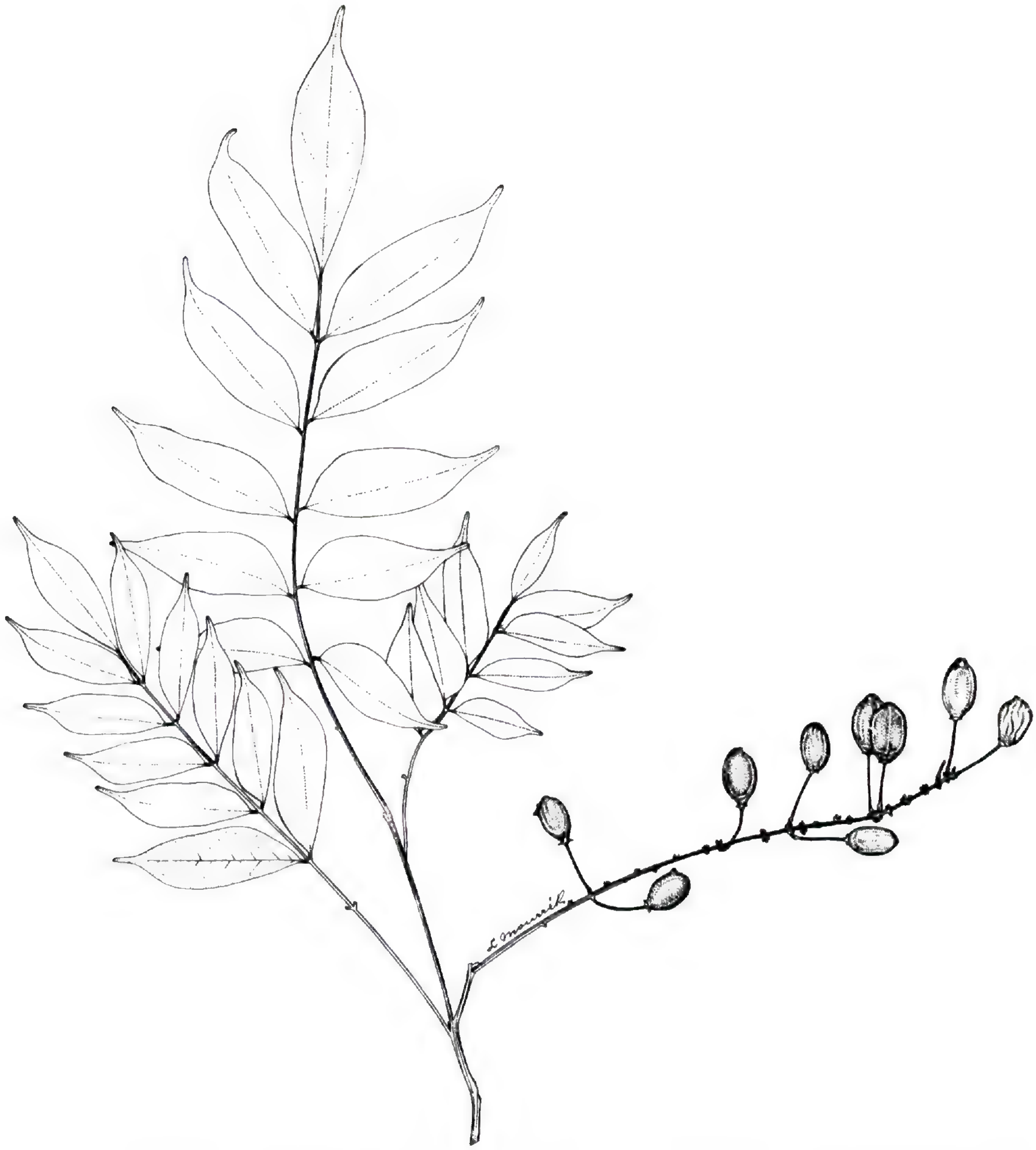

FIGURE 4. *Picramnia allenii* D. M. Porter, habit (× ½). [After *Hunter & Allen 306* (MO).]

Mountains beyond La Pintada, 400–600 m, *Hunter & Allen* 538 (MO, holotype; F, GH, NY, US, isotypes).

Picramnia allenii occurs in wet forests and is either able to persist when they are felled or to invade such disturbed areas. Known as "amargocito" (fide *von Hagen & von Hagen 2126*).

2. **Picramnia cooperi** D. M. Porter, Jour. Arnold Arbor. 54: 317. 1973.

Shrubs or small trees, 2–10 m high; branchlets yellowish appressed-pubescent, becoming glabrate. *Leaves* alternate, pinnate, ca. 25 cm long; petiole and the rachis sparingly appressed-pubescent, becoming glabrate; leaflets 7–8, alternate

to subopposite, ovate to elliptic or oblong, acute to obtuse and abruptly acuminate apically, rarely retuse, acute to obtuse and inequilateral basally, the margins entire, revolute, chartaceous, the blade sparingly appressed-pubescent, especially basally, on the veins beneath, and marginally, becoming glabrate, 5–12 cm long and 21–53 mm wide, the terminal and subterminal leaflets largest, the petiolules pubescent, ca. 3 mm long. *Staminate racemes* axillary, aggregated or solitary, simple, densely-flowered, yellowish appressed-pubescent, 68–96 cm long. *Staminate flowers* 3-merous, numerous, several together in clusters, cream-colored, the pedicels sparingly yellowish appressed-pubescent, to ca. 1 mm long; sepals 3, broadly ovate, yellowish appressed-pubescent, 2 mm long and 1.5 mm wide; petals 3, oblanceolate, apiculate, hooded, glabrous, longer than the sepals, ca. 2 mm long; stamens 3, exserted, the filaments subulate, glabrous, 3 mm long; disc 3-lobed, each lobe in turn bilobed and extending between 2 stamens; ovary conical, glabrous, the style and stigma absent. *Carpellate racemes*, *flowers*, and *fruits* unknown.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1226*, in part (MO). Region of Almirante, Daytonia Farm, *Cooper 375* (GH, holotype; F, NY, US, isotypes).

Picramnia cooperi is a shrub or small tree of the rain forest. It superficially resembles *P. latifolia* but is easily distinguished by its leaflet pubescence, 3-merous flowers, and much larger inflorescences.

3. **Picramnia carpinterae** Polak., Linnaea 41: 553. 1877.

Picramnia antidesma var. *carpinterae* (Polak.) O. Ktze., Rev. Gen. Pl. 1: 104. 1891.

Small trees, 5–12 m high, the crown flat; branchlets yellowish-villous. *Leaves* alternate, pinnate, to 20 cm long; petiole and the rachis yellowish-villous; leaflets 9–11, alternate to subopposite, obtuse or acute and acuminate apically, more or less inequilateral, the uppermost and middle leaflets elliptic to ovate and cuneate basally, the lowermost ovate and cordate basally, paler beneath, the margins repand, revolute, subcoriaceous, villous marginally and beneath, especially on the veins, to 11 cm long and 5.5 cm wide, the lowermost pair much smaller than the others, the petiolules villous, 1–2 mm long. *Staminate racemes* subterminal, becoming axillary, solitary, simple, yellowish-villous, 14–22 cm long. *Staminate flowers* 3-merous, numerous, 1-several aggregated in clusters, the pedicels glabrous, 1–3 mm long; sepals 3, obovate, sparingly pubescent, 1.5 mm long and 1 mm wide; petals 3, narrowly obovate, ca. 1 mm long; disc 3–4-lobed; stamens 3(–4), exserted, the filaments subulate, glabrous, ca. 2.5 mm long, ovary rudimentary, conical, villous apically, the style and stigma absent. *Carpellate racemes* solitary, yellowish-villous, 23–27 cm long in flower, to 30 cm long in fruit. *Carpellate flowers* 3-merous, white, the pedicels villous to glabrate, 2–4 mm long in flower, 4–12 mm long in fruit, articulated basally; sepals 3, broadly triangular, densely villous, persistent and spreading in fruit, ca. 1.5 mm long and 1.5 mm wide; petals 3, narrowly obovate, apiculate, spreading, ca. 2 mm long; staminodes 3, opposite the petals; disc 3-lobed, glabrous; ovary ovoid, densely pubescent, 1–2 mm high, 2-loculed, the ovules 2 per locule, the style bilobed, the lobes recurved and persisting in fruit. *Berries* red, ellipsoid, sparingly pubescent; seeds 1–2.

Costa Rica and Panama. In Panama known to flower in March, and to fruit in March and August.

CHIRIQUÍ: Bajo Chorro, rain forest, 6000 ft, *Davidson 407* (A, F, MO, US). Boquete, *Seemann 1252* (NY, photo from K). Forests around Boquete, 1000–1300 m, *Pittier 2985* (F, US). Cerro Horqueta, dense woodland in cloud forest, 5000–6000 ft, *Dwyer & Hayden 7697* (MO). Forests along Río Ladrillo and vicinity, above Boquete, 1200–1300 m, *Pittier 3053* (F, GH, US).

Picramnia carpinterae is a plant of cloud forests.

4. **Picramnia dwyeri** D. M. Porter, Jour. Arnold Arbor. 54: 319. 1973.

Shrubs or small trees, ca. 2 m high; branchlets densely yellowish-tomentose, finally becoming glabrate. *Leaves* alternate, pinnate, to 24 cm long; petiole and the rachis densely yellowish-tomentose; leaflets ca. 8–13(–17), alternate, the lowermost subopposite, ovate to obovate or oblanceolate, the terminals elliptic, abruptly short-acuminate apically, markedly inequilateral basally, the margins entire, revolute, chartaceous, the midrib indented above and prominent beneath, appressed yellowish-pubescent on the margin and on the midrib beneath, minutely puberulent in the sulcus above, the blade sparingly pubescent beneath, to 5(–8.8) cm long and 2(–4.5) cm wide, the terminal leaflets largest, the lowermost smallest and reflexed, the petiolules densely yellowish-tomentose, 1–2 mm long. *Staminate racemes* terminal, aggregated, simple, yellowish appressed-pubescent, to 20 cm long. *Staminate flowers* 4-merous, 1–2 together, green, the pedicels spreading, sparingly pubescent, 1–1.5 mm long; sepals 4, connate basally, narrowly ovate, apiculate, yellowish appressed-pubescent, ca. 1.5 mm long; petals 4, narrowly lanceolate, glabrous, a little longer than the sepals, 2 mm long; stamens 4, exserted, the filaments subulate, glabrous, adnate basally to the petals, ca. 3 mm long, the anthers basifixed, 2-lobed, the lobes separated; ovary rudimentary, tomentose, the style and stigma absent. *Carpellate racemes* terminal, solitary, simple, densely appressed yellowish-pubescent, to 32 cm long in fruit. *Carpellate flowers* 4-merous, in clusters of 3 that alternate on the inflorescence, usually only 1 of the 3 forming a fruit, the pedicels thickened apically, appressed yellowish-pubescent, articulated basally, 3–8 mm long in fruit; sepals 4, triangular, acute, appressed yellowish-pubescent, persistent and spreading in fruit; petals 4, narrowly triangular, shorter than the sepals; style bilobed, the lobes recurved and persisting in fruit. *Berries* green maturing red, obovoid or rarely ellipsoid, appressed-pubescent, 2-loculed, 7–15 mm long; seeds 1–2.

Endemic. Known to flower in September, and to fruit in February and July through September.

DARIÉN: Bolamina, small hill, *Duke & Bristan 388* (MO). Near Refugio, 15–21 mi. N of Santa Fé, ca. 30 m, *Duke 10303* (MO). Río San José, *Duke & Bristan 416* (MO). Río Tuira, between Río Paya and Río Pucro, *Duke & Kirkbride 14054* (F, MO). Teotuma, ca. 100 m, *Duke 10061* (MO). PANAMÁ: Between Cañasas and Sabalo, ca. 100 m, *Duke 14456* (MO, holotype). SAN BLAS: Río Chucunaque, 2–10 mi. above Cuna–Darién Boundary, *Duke 8567* (MO). VERAGUAS: Isla de Coiba, *Dwyer 2333* (MO, SIU), *2337* (MO).

Picramnia dwyeri is an understory shrub or small tree in monsoon forests. It is known as "korbugia" and "pakaburwi" by the Bayano Cuna Indians (fide *Duke 14456*). The berry "has bad taste" (fide *Duke & Bristan 388*).

5. **Picramnia latifolia** Tul., Ann. Sci. Nat. Bot., Sér. 3. 7: 258. 1847.

Picramnia umbrosa Seem., Bot. Voy. Herald 97. 1854.

Slender *shrubs or small trees*, 3.5–7 m high; branchlets appressed-puberulent, becoming glabrate. *Leaves* alternate, pinnate, 21–32 cm long; petiole and the rachis sparingly appressed-puberulent, becoming glabrate; leaflets (3–)6–8(–9), mainly an odd number, alternate, ovate to elliptic or oblong, obtuse or acute and abruptly acuminate apically, rarely retuse, acute and slightly inequilateral basally, the margins entire, revolute, chartaceous, the blade sparingly appressed-puberulent, especially basally, becoming glabrate, 4–17 cm long and 2–8.5 cm wide, the petiolules sparingly pubescent to glabrate, 3–4 mm long. *Staminate racemes* axillary, aggregated, simple or rarely branched basally, densely-flowered, minutely yellowish appressed-puberulent, 10–21 cm long. *Staminate flowers* 5-merous, numerous, 1–3 together in clusters, white or green, the pedicels minutely yellowish appressed-puberulent, to ca. 1 mm long; calyx cup-shaped, 5-lobed, minutely yellowish appressed-puberulent, ca. 1 mm high, the lobes ovate-triangular; petals 5, elliptic, acuminate, glabrous, longer than the calyx-lobes, 1 mm long; stamens 5, exserted, the filaments filiform, glabrous, inserted at the bases of the petals between the ovary-lobes, more than twice as long as the calyx, ca. 2–3 mm long; ovary conical, 5-lobed, tomentose apically, ca. 1 mm high, the style and stigma absent. *Carpellate racemes* aggregated, appressed yellowish-puberulent, to 23 cm long in flower, to 65 cm long in fruit. *Carpellate flowers* 5-merous, whitish, the pedicels appressed yellowish-puberulent, ca. 1 mm long; sepals 5, triangular, appressed yellowish-puberulent, persistent and spreading in fruit, ca. 1.5 mm long; petals 5, ovate, shorter than the sepals, ca. 1 mm long; stamens absent; disc annular; ovary ovoid, densely appressed-puberulent, 1–2 mm high, the style bilobed, the lobes recurved and persisting in fruit. *Berries* pink to bright red, yellow, or orange, ellipsoidal to globose, minutely appressed-puberulent, 2–3-loculed, to 1 cm long; seeds 1(–2–3).

Costa Rica, Panama, and Colombia. In Panama known to flower from December through March, and to fruit in February, March, May, and June.

BOCAS DEL TORO: Almirante region, *Cooper & Slater 64* (US). Changuinola Valley, *Dunlap 450* (F, GH, US), *548* (F, US); Farm Six, *Dunlap 492* (F, US). Vicinity of Chiriquí Lagoon, *von Wedel 1226*, in part (MO). CANAL ZONE: Barro Colorado Island, cove of dock, *Croat 13819* (MO), forest N of clearing, *Croat 14575* (MO); SE of Armour 7, *Foster 909* (DUKE, F); N of Armour 10, *Foster 871* (DUKE); Central Cove, end of Peña Blanca Peninsula, *Croat 5447* (MO, NY, SCZ); along trail to Fuertes House, *Croat 5263* (MO, SCZ); head of Lutz stream between Barbour Trail 200–422, *Croat 5676* (MO); shore of Peña Blanca, *Woodworth & Vestal 676* (A, MO); Peña Blanca Point, *Croat 5553* (MO); in front of Redwood House, end of Armour Trail, *Wetmore & Abbe 193* (A, GH, MO); Wheeler Trail, *Robyns 65-13* (MO). Canal Zone Experiment Gardens, *Lindsay 324* (US). On the Chagres, forests between Juan Mina and El Vigía, Panamá, 20–80 m, *Pittier 2399* (GH, NY, US). Gatún, *Hayes 623* (NY, US). Madden Dam, *Dwyer 8385* (MO). Pipeline Road, 2.5 mi. from gate, *Croat 9353* (F, MO, SCZ). Moist woods, Río Paraíso, above East Paraíso, *Standley 29921* (MO, US). CHIRIQUÍ: Vicinity of San Felix, 0–120 m, *Pittier 5186* (F, NY, US). DARIÉN: Cerro Pirre, *Bristan 564* (MO). Cerro Yaviza River, near Yaviza, *Duke & Bristan 423* (MO). In forests, around Garachiné, near sea level, *Pittier 5514* (F, US). Trail between Pinogana and Yaviza, ca. 15 m, *Allen 250* (A, F, MO). Seasonal deciduous forest, between Río Perecenico and Rancho Frío, 500–2500 ft, *Duke & Elias 13881* (GH, MO). Río Pirre, 2–5 mi. above El Real, *Duke 4903* (MO). LOS SANTOS: E of Cambutal, near coast, *Holdridge 6221* (MO). Forest of

espavé, caoba, and cedro espino, Guanico, vicinity of Tonosí, 117 ft, *Stern et al. 1844* (MO, US). PANAMÁ: Moist forest, Río Tapia, *Standley 28043* (US). SAN BLAS: High hills back of Puerto Obaldía, 50–200 m, *Pittier 4291* (F, GH, NY). VERAGUAS: Tonosí, *Mell*, 1922 (NY).

Picramnia latifolia is widespread throughout lowland Panama, occurring in monsoon forests and deciduous seasonal forests. Known as "bichichi" (fide *Duke & Bristan 423*) and "canjura" (fide *Holdridge 6221*). The berries are edible (fide *Duke 4903* and *Duke & Bristan 423*), although *Croat 5263* reports them to be "infested with large ants."

6. **Picramnia corallodendron** Tul., Ann. Sci. Nat. Bot., Sér. 3. 7: 259. 1847.

Small trees; branchlets yellowish appressed-tomentulose. *Leaves* alternate, pinnate, 17–27 cm long; petiole and the rachis yellowish appressed-tomentulose; leaflets 10–15, mainly an even number, alternate to subopposite, elliptic or the lowermost ovate, narrowly short-acuminate apically, acute or rounded and markedly inequilateral basally, the margins entire, revolute, chartaceous, yellowish appressed-tomentulose above and beneath on the main vein and marginally, the blade sparingly pubescent, soon glabrate, 26–115 mm long and 11–35 mm wide, the terminal leaflets largest, the lowermost smallest and reflexed, the petiolules yellowish appressed-tomentulose, 1–2 mm long. *Staminate racemes* and *flowers* unknown. *Carpellate racemes* solitary or in pairs, yellowish appressed-tomentulose, 28–40 cm long. *Carpellate flowers* 5-merous, apparently subopposite in pairs, only 1 of a pair forming fruits, the pedicels yellowish appressed-puberulent, thickened apically, articulated basally, ca. 1 cm long in fruit; sepals 5, lanceolate, apiculate, appressed-puberulent, connate basally, persistent and appressed in fruit, 1.5–2 mm long and less than 1 mm wide; petals 5, linear, ca. as long as sepals; ovary obovoid, densely appressed-puberulent, 2-loculed, ovules 2 per locule, the style bilobed, appressed-puberulent basally, the lobes ca. 1.5 mm long, recurved and persisting in fruit. *Berries* red, obovoid, appressed-puberulent, ca. 1.5 cm long; seed 1.

Panama, Colombia, and Peru; perhaps also in Ecuador and Bolivia. In Panama known to fruit in September.

PANAMÁ: Woods along PanAmerican Highway ca. halfway between El Llano and Río Mamoni, *Duke 5649* (F, MO).

Picramnia corallodendron apparently is a plant of monsoon forests. It has not hitherto been reported from Panama.

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Simarouba 24†, **29**
amara **30**, 32†
—var. opaca 30
—var. typica 30
glauca 32†
opaca 30
Simaroubaceae **23**
Tariri 32
Zwingera 27
amara 30

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 168. VERBENACEAE

HAROLD N. MOLDENKE[2]

Herbs, shrubs, woody vines, or trees; no pneumatophores present; branches, branchlets, and twigs mostly tetragonal, not prominently nodose or articulate, often annulate. *Leaves* mostly decussate-opposite, sometimes whorled, alternate, or scattered, thick- or thin-textured, deciduous, exstipulate, sessile or petiolate, simple or sometimes palmately- (rarely pinnately-) compound or 1-foliolate, the blades entire or variously dentate, incised, or cleft. *Inflorescences* axillary or terminal, determinate and centrifugal (cymose) or indeterminate and centripetal (racemose), in the form of cymes, racemes, spikes, panicles, thyrsi, heads, or false-umbels, sometimes involucrate, the axillary inflorescences mostly solitary. *Flowers* sessile or pedicellate, perfect or imperfect, hypogynous, sometimes heterostylous or polygamous, large or small, mostly irregular, not individually involucrate; calyx gamosepalous, campanulate, tubular, or salverform, persistent, usually accrescent, 4(2, 5, or 7)-lobed or toothed or sometimes subentire; corolla regular or irregular, gamopetalous, funnel- or salverform, usually with a well-developed tube, the limb 4, 5(7–many)-parted, often somewhat 2-lipped; stamens mostly 4 and didynamous or reduced by abortion to 2, sometimes 4 or 5 and equal, inserted on the corolla-tube; staminodes often present; gynoecium 2(4–5)-carpellate, syncarpous, 1 carpel sometimes aborted, the ovary mostly compound, sessile, or sometimes subtended by a disc, mostly somewhat 4-lobed, at first 2–5-loculed, usually soon becoming 4–10-loculed through formation of false partitions, never with a free central placenta or columella, the axile placenta-lobes each bearing 1 anatropous and basal or hemianatropous and lateral ovule, so that locules not subsequently divided by partitions each contain 1 ovule. *Fruit* usually a dry schizocarp, or drupaceous with a thick and dry or fleshy exocarp and more or less hard endocarp, 2–4-loculed and indehiscent when mature or dehiscent into 2(–4–10), 1- or 2-loculed pyrenes; seeds plainly testate, the embryo never viviparous, the radicle short and inferior, glabrous, the cotyledons 2, flat, more or less thickened, parallel.

A widely distributed and complex family of about 76 genera and 3435 specific and subspecific taxa, found in all portions of the world except the driest and

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[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

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ANN. MISSOURI BOT. GARD. 60: 41–148. 1973.

hottest parts of the Sahara Desert and in the Arctic and Antarctic regions, most abundant in the tropics. The family is closely related to the Lamiaceae from which it is distinguished with difficulty. Numerous ornamental, medicinal, and otherwise economic forms are included in the family.

In addition to herbaria assigned acronyms by the International Bureau of Plant Taxonomy and Nomenclature, material has been cited from the following herbaria: LEMPBERG—Fritz Lempberg Herbarium, Hatzendorf, Steiermark, Austria; BARRO—Canal Zone Biological Area Herbarium, Barro Colorado Island, Canal Zone; MOLDENKE—H. N. Moldenke Herbarium, Plainfield, New Jersey, U.S.A.

a. Inflorescence capitate, spicate or racemiform, indeterminate and centripetal.
  b. Inflorescence spicate, often subcapitate in anthesis and elongating in fruit; flowers sessile or subsessile.
    c. Fruit with 4 1-seeded locules becoming dry schizocarps ..... 1. *Verbena*
    cc. Fruit with 2, 1- or 2-seeded pyrenes (or by abortion only 1).
      d. Pyrenes 1-loculed and 1-seeded, fruit separating or not.
        e. Perfect stamens 4.
          f. Calyx truncate or shallowly toothed; corolla 4–5-lobed; fruit drupaceous, usually with a fleshy and juicy exocarp and hard endocarp, either 2-loculed or separating into 2, 1-loculed pyrenes ..... 2. *Lantana*
          ff. Calyx 2–4-cleft or conspicuously toothed; corolla 4-lobed; fruit dry, with a hard and thin or papery exocarp, separating into 2, 1-loculed pyrenes.
            g. Mostly herbaceous, with trailing or ascending stems, rooting at the nodes, sometimes somewhat woody; spikes greatly elongating in fruit; bractlets cuneate-obovate, not 4-ranked; trichomes malpighiaceous (medifixed) ..... 3. *Phyla*
            gg. Erect bushes, subshrubs, shrubs, or trees; spikes not usually elongating in fruit; branchlets mostly ovate or lanceolate; often more or less 4-ranked; trichomes not malpighiaceous ..... 4. *Lippia*
        ee. Perfect stamens 2, with a posterior pair of staminodes ..... 5. *Stachytarpheta*
      dd. Pyrenes 2-loculed and 2-seeded (or by abortion 1-loculed and 1-seeded), fruit not separating.
        h. Woody bushes or shrubs; fruit usually fleshy and juicy; flowers in dense spikes or heads ..... 2. *Lantana*
        hh. Herbs; fruit dry; flowers in loose spikes or racemes ..... 6. *Priva*
  bb. Inflorescence racemiform and elongate, or reduced and axillary; flowers plainly pedicellate.
    i. Woody vines; fruit with 2-loculed and 1-seeded pyrenes; mature fruiting-calyx usually conspicuously 5-winged, wings greatly enlarged, stiff, dry, net-veined, and often colored; epicalyx present ..... 7. *Petrea*
    ii. Trees or shrubs; fruit with 2 or 4, 2-loculed and 2-seeded pyrenes, or less by abortion; mature fruiting-calyx not winged; no epicalyx present.
      j. Drupes with 4 pyrenes, each 2-loculed and 2-seeded; calyx mostly obvolute and rostrate (enveloping the fruit) after anthesis ..... 8. *Duranta*
      jj. Drupes with 2 pyrenes, each 2-loculed and 2-seeded (or 1-seeded by abortion); calyx not obvolute nor rostrate after anthesis ..... 9. *Citharexylum*
aa. Inflorescence cymose, determinate and centrifugal, the cymes often congested into panicles, false umbels, umbelloid panicles, thyrsi, or heads, when axillary sometimes reduced to 1 flower.
  k. Flowers essentially regular; stamens 4–6, equal.
    l. Drupes normally with 4 or 5, 1-loculed and 1-seeded pyrenes; fruiting-calyx not inflated.
      m. Stigma deeply bifid with long awl-shaped branches; flowers diclinous; fruiting-calyx enlarged and indurated; stamens inserted at or above the middle of the corolla-tube; ovary mostly glabrous ..... 10. *Aegiphila*

mm. Stigma depressed-capitate or peltate; flowers mostly polygamous; fruiting-calyx usually unchanged and patelliform; stamens inserted at or near the base of the corolla-tube; ovary usually more or less pubescent ..... 11. *Callicarpa*
ll. Drupes with 1, 4-loculed pyrene; fruiting-calyx conspicuously inflated .... 12. *Tectona*
kk. Flowers (especially the corolla) more or less irregular; stamens 4, didynamous.
n. Drupes with 1, 4-loculed pyrene.
o. Fertile stamens 2; filiform staminodes present; leaves simple ..... 13. *Cornutia*
oo. Fertile stamens 4; usually no staminode present; leaves palmately compound, rarely 1-foliolate ..... 14. *Vitex*
nn. Drupes with 4 (or less through abortion), 1-loculed pyrenes ..... 15. *Clerodendrum*

1. VERBENA

Verbena L., Sp. Pl. 18. 1753; Gen. Pl., ed. 5. 12. 1754.

Obletia Lemon. *ex* Rozier, Introd. Obs. Phys. Hist. Nat. 367. 1773.
Patya Neck., Elem. Bot. 1: 296. 1790.
Glandularia J. F. Gmel. *in* L., Syst. Nat., ed. 13. 2(2): 920. 1791.
Billardiera Moench, Meth. Pl. 369. 1794.
Shuttleworthia Meisn., Pl. Vasc. Gen. 1: 290 & 2: 198. 1839.
Uwarowia Bunge, Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 7: 278. 1840.
Aubletia Jacq. *apud* Wittstein, Etymolog.-bot. Handwörterb. 85. 1852.
Uerbena Sessé & Moc., Pl. Nov. Hisp. 1: 6. 1887.
Helleranthus Small, Fl. Southeast. U. S., ed. 1. 1011 & 1337. 1903.
Canadea Patermann, Beitr. Zytol. Verbenac. 13, 43 & [54], *pl. 1, fig. 1 & 2*. 1935.

Herbs, sometimes slightly woody basally; stems and branches procumbent, ascending, or erect, glabrous or variously pubescent. *Leaves* mostly decussate-opposite, rarely whorled, dentate (rarely entire) or variously lobed, incised, or pinnatifid. *Inflorescences* spicate; spikes terminal, usually densely many-flowered, often flat-topped and pseudo-umbellate or fasciculate-capitate, sometimes greatly elongate with densely crowded or scattered flowers, rarely also axillary, often greatly elongating only after anthesis. *Flowers* small or medium-sized, each solitary and axillary in a usually narrow bractlet; calyx usually tubular, 5-angled, 5-ribbed, unequally 5-toothed, not at all or but slightly changed in fruit, then herbaceous, mostly ventricose, eventually split, often connivent or contorted apically, thin-textured; corolla salverform or funnelform, the tube cylindric, straight or curved, often slightly ampliate or subinflated apically, usually villous at the stamen-insertion within and barbate at the mouth, the limb flat, spreading or oblique, weakly 2-lipped, the lobes 5, usually elongate, more or less unequal, varying from obtuse or rounded to emarginate apically, the 2 posterior outermost and the anterior innermost in prefloration; stamens 4, didynamous, inserted in the upper half of the corolla-tube, included, the anthers ovate, with 2 parallel or slightly divergent thecae, dehiscing longitudinally, the dorsal connective un-appendaged and narrowly muticous or provided with a more or less conspicuous glandular appendage; gynoecium 2-carpelled, the ovary superior, entire or 4-lobed, apically situated on a somewhat lobed annular disc, completely 4-loculed even at anthesis, the ovules 1 per locule, attached laterally at or near the base, erect, anatropous; the style usually short and equaling the stamens, somewhat dilated, shortly 2-lobed or bifid apically, the anterior lobe or branch stigmatiferous and subpulvinate-papillose, the posterior lobe or branch smooth and horny and non-stigmatiferous, not as broad as the anterior. *Fruit* mostly enclosed by the mature calyx, schizocarpous, the pericarp hard and dry, readily separating at maturity

into 4, 1-seeded linear or linear-oblong (rarely elliptic-winged) crustaceous nutlets; seeds 4, erect, oblong, triangular in cross-section, without or with negligible endosperm, the outer face convex, the cotyledons 2, thick, applicate.

A complex genus of 392 specific and subspecific taxa native to temperate and tropical America, two species native to the Mediterranean region and the Near East, and introduced elsewhere in the Old World. There are several widely cultivated forms and numerous natural and artificial hybrids. Several American species have become naturalized in various parts of Europe, Asia, Africa, and Australia. *Glandularia* is perhaps worthy of generic segregation.

a. Spikes densely congested with usually closely imbricate flowers; stems and peduncles densely hirsute or villous; calyx 5–6 mm long; corolla 1–2.5 cm wide ..... 1. *V. hybrida*
aa. Spikes elongate and loosely flowered when mature; stems and peduncles scabridulous or subglabrate; calyx 2–2.5 mm long; corolla 2.5–3 mm wide ..... 2. *V. litoralis*

1. **Verbena hybrida** Voss *ex* Rümpler, Vilm. Illustr. Blumeng., ed. 1. 1263. 1873.

V. hortensis Vilm., Fleures Pleine Terre, ed. 5. 1126. 1909.

Perennial *herbs*, usually treated as annuals in temperate-climate gardens, half-hardy in protected places, of spreading or compact growth, 15–45 cm high when in bloom; stems mostly procumbent, trailing or creeping, or ascending in compact forms, sometimes forming perennial mats 1 m wide in warm climates, slender, tetragonal, usually 30–60 cm long, occasionally to 1 m, densely hirsute or villous; branches numerous, decumbent or ascending, more or less densely soft-hirsute or villous with spreading trichomes. *Leaves* numerous, the blades chartaceous, usually thick-textured, rather uniformly dark-green on both surfaces or somewhat lighter beneath, often variegated with yellow, rarely entirely chlorotic, those at the tips of the branches smaller, 1.3–8.3 cm long and 1–5.8 cm wide, acute apically, usually truncate or subtruncate basally or cuneately narrowed into the petiole, irregularly incised-dentate from apex to base with numerous acute and spreading, often lobe-like and doubly dentate teeth, more or less densely soft-pubescent or hirsutulous on both surfaces with rather coarse whitish trichomes antrorsely strigose above and usually spreading from the midrib and larger veins beneath; petioles slender, 2–7 mm long, densely hirsute with spreading white trichomes, margined. *Inflorescences* terminal, large and showy, varying from an extremely flattened corymb to a very long spike, the floriferous portion 4.5–6.5 cm long and 5.5–9 cm wide, 28–55-flowered; spikes at first depressed and corymb- or fascicle-like, later elongating, densely many-flowered; peduncles tetragonal, 3–10 or more cm long, densely white-hirsute or -villous; bractlets lanceolate, much shorter than the calyx, 5–6 mm long, attenuate apically, densely soft-pubescent with whitish trichomes. *Flowers* closely imbricate and often more or less fragrant; calyx tubular, 0.8–1.5 cm long, 5-costate and -plicate, densely white-hirsutulous, varying from subtruncate and merely undulate to shortly 5-apiculate; corolla hypocrateriform, large and showy, white or cream to practically all shades of red, yellow, blue, and purple, usually with a white, cream, or yellow spot in the center of the limb and with or without a colored inner rim, sometimes striped, the tube 1.5–3 cm long, usually greenish or whitish, glabrous or obscurely pilosulous, the limb 1–2.5 cm wide; anthers not appendaged.

An extremely polymorphic hybrid, planted for ornament practically throughout the world, often tending to escape or persist after cultivation in warmer areas.

The exact ancestry of the plant is not certain, but it is supposed to be a multiple hybrid between *Verbena platensis* Spreng., *V. phlogiflora* Cham., *V. incisa* Hook., and *V. peruviana* (L.) Britton, all natives of South America. Hundreds of cultivar names, including many in Latin form, exist in the horticultural literature.

PANAMÁ: Sabanas, Panamá, *Bro. Paul 39* (US). Cultivated, Panamá, *Bro. Maurice 896* (US).

Known as "malvina" (fide *Bro. Paul 39*).

2. **Verbena litoralis** B.H.K., Nov. Gen. Sp. Pl., ed. folio. 2: 223, *pl. 137*. 1817. —FIG. 1.

V. lanceolata Willd. *ex* Spreng. *in* L., Syst. Veg., ed. 16. 2: 748. 1825.
V. affinis Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(2): 322. 1844.
V. bonariensis β littoralis Hook. *ex* C. Mull. *in* Walp., Repert. Bot. Syst. 4: 20. 1845.
V. littoralis var. *glabrior* Benth., Bot. Voy. Sulphur 153. 1846.
V. littoralis β leptostyachya Schau. *in* A. DC., Prodr. 11: 542. 1847.
V. nudiflora Nutt. *ex* Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(2): 195. 1863.
V. hansenii Greene, Pittonia 3: 308. 1898.
V. parviflora Larrañ., Escritos D. A. Larrañ. 2: 9. 1923.

Quick-growing erect or suberect perennial herbs, 0.2–2 m high, sometimes large and robust, woody-based, fastigiately few- to many-branched above, glabrous and shiny or sparingly strigillose; stems to 12 mm thick, tetragonal or subtetragonal in cross-section, the internodes deeply sulcate above the insertion of the leaves and faintly many-sulcate between, scabridulous on the angles when young, green, slightly contracted at the nodes. *Leaves* with the blades lanceolate to oblong or oblanceolate, 3–10 cm long and 1–1.5 cm wide, acute apically, tapering into a short petiole basally or sessile to subsessile, acuminate and somewhat clasping basally, scabridulous throughout or scabrous and somewhat rugose only above, the upper ⅔ more or less sharply and coarsely serrate with commonly 3–5 somewhat mucronate teeth per side, sparsely strigillose on both surfaces, the venation impressed above and prominent beneath. *Inflorescences* terminal spikes, several to many, pedunculate, cymose or corymbose-paniculate, slender or filiform, pilosulous, at first congested and about 4 mm in diameter, dense or interrupted, later loosely flowered and elongate, in fruit becoming 2–8 cm long, the fruits usually not contiguous; bractlets ovate-lanceolate, marcescent, rigid, acuminate or subulate, 1–3 mm long, usually subequaling or somewhat shorter than the calyx, abruptly upcurved, glabrate. *Flowers* with the calyx often purple, 2–2.5 mm long, pubescent or finely strigillose, the rim subtruncate, the 5 teeth equal, minute, subulate; corolla ca. 3 mm long, various shades of blue, violet, or purple, puberulent, the tube greenish toward the base, variable in length, always somewhat longer than the calyx, the limb inconspicuous, 2.5–3 mm wide, puberulent on the inner surface, the lobes subequal, obtuse, glabrous; anthers greenish-yellow; ovary almost 1 mm long, green, glabrous, the style ca. 1 mm long. *Fruits* with the nutlets trigonous, dark-stramineous, linear-oblong, 1–1.9 mm long, glabrous, striate, somewhat reticulate, the commissural face about as long as the nutlet, muricate-scabrous.

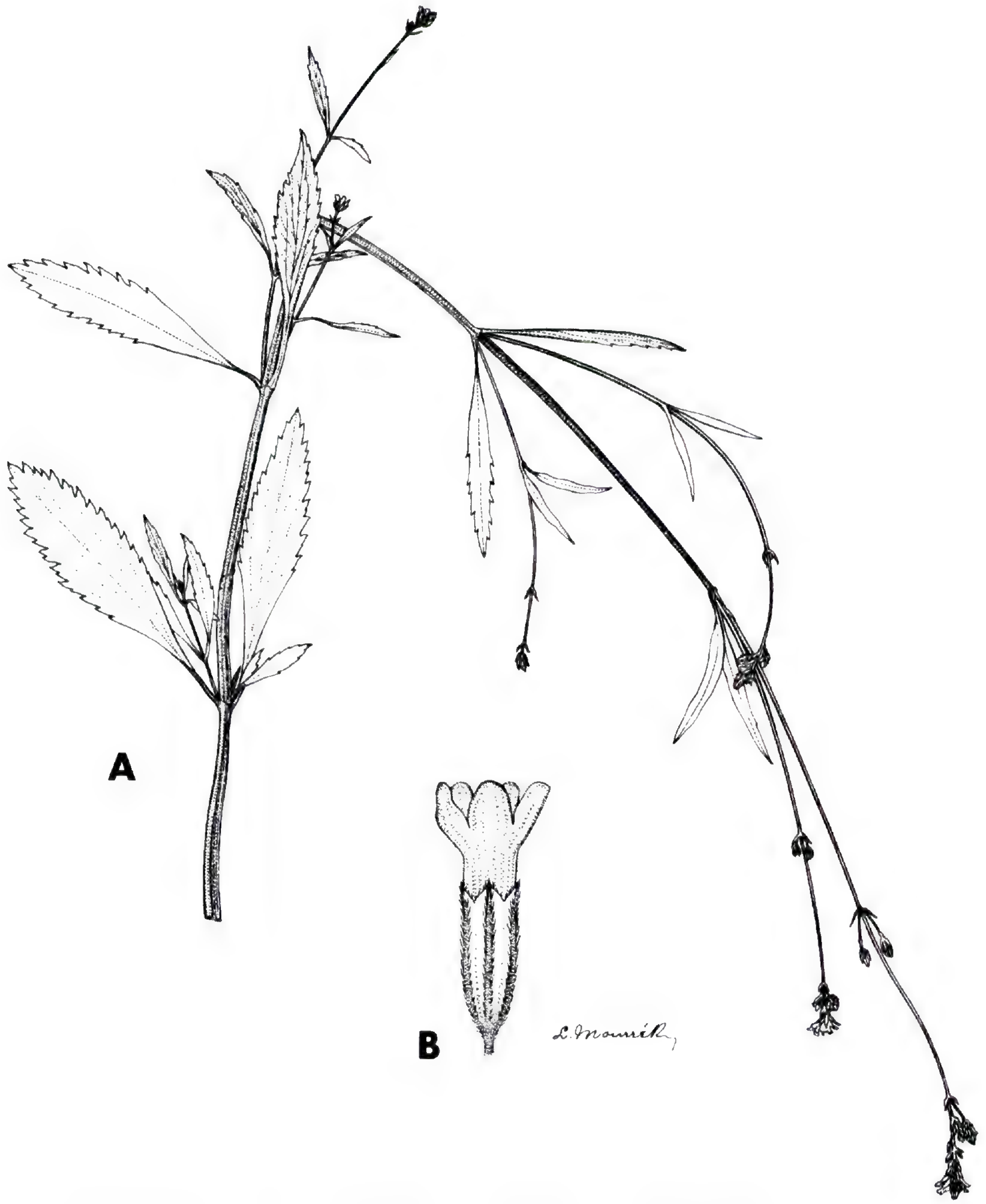

FIGURE 1. *Verbena litoralis* H.B.K.—A. Habit (× 5/8).—B. Flower (× 7½). [After *Tyson 5627* (MO).]

A widely distributed and extremely polymorphic subtropical and tropical weed, ranging from the southern United States throughout Central and South America; introduced in Oregon, California, South Africa, Hawaii, Australia, and parts of Oceania.

CHIRIQUÍ: Grassland and wayside weed, Alto Lino, vicinity of Boquete, 960 m, *Bro. Maurice 687* (US). Wet roadside in sun, Bambito, 1 mi. SW of Cerro Punta, 5600 ft, *Tyson 5627* (MO). Common, 5600 ft, *Tyson 5675* (MO). In second growth, cultivated areas, and roadsides, from Boquete to 3 mi. N, 3300–4200 ft, *Lewis et al.* 339 (MO, US). Fields along Río

Caldera above Boquete, 1300–1350 m, *Killip 3510* (US). Vicinity of Casita Alta, Volcán de Chiriquí, ca. 1500 to 200 m, *Woodson et al. 858* (MO, NY). Dense woodland in cloud forest, Cerro Horqueta, Boquete, 5000–6000 ft, *Dwyer & Hayden 7738* (MO). Along stream near trail N of Cerro Punta, *Croat 10444* (NY). In grassy swales, vicinity of Cerro Punta, 1500–2000 m, *Seibert 251* (NY). Hillside, vicinity of Monte Lirio, valley of upper Río Chiriquí Viejo, 1300–1900 m, *Seibert 169* (MO, NY). Vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1412* (MO, NY). Valley of Río Chiriquí Viejo N of Volcán City, 5000–5600 ft, *Duke 9072* (MO). PANAMÁ: Cerro Jefe, *Tyson et al. 4300* (MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2409* (MO).

2. LANTANA

Lantana L., Sp. Pl. 626. 1753; Gen. Pl., ed. 5. 275. 1754.

Camara L., Gen. Pl., ed. 5. 275. 1754, *pro syn.*
Kamara Adans., Fam. Pl. 2: 12. 1763.
Charachera Forsk. *ex* Bartl., Ord. Nat. Plant. 178. 1830.
Riedelia Cham., Linnaea 7: 240. 1832.
Tamonopsis Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 246. 1874.

Erect *herbs* or *shrubs*, sometimes subscandent, scandent, or prostrate, usually more or less scabrous and hirtous-pubescent or tomentose with simple trichomes. *Leaves* opposite or ternate (rarely quaternate), dentate, often rugose. *Inflorescences* dense cylindric spikes or contracted to form heads, usually axillary, pedunculate. *Flowers* sessile, borne in the axils of solitary, oblong, lanceolate, or ovate, often apically acuminate, and spreading or subimbricate bractlets. *Flowers* with the calyx small, membranous, truncate and entire or sinuate-dentate; corolla hypocrateriform, red or yellow to blue or white, the tube cylindric, slender, equal in diameter throughout or slightly ampliate above, the limb spreading, regularly or obscurely 2-lipped, 4–5-fid, the lobes broadly obtuse or retuse apically; stamens 4, didynamous, inserted at about the middle of the corolla-tube, included, the anthers ovate, with parallel thecae; gynoecium 1-carpelled, the ovary 2-loculed, the ovules 1 per locule, basal and erect or attached laterally near the base of each locule, the style usually short, the stigma rather thick, oblique or sublateral. *Fruits* drupaceous, the exocarp usually more or less fleshy (rarely dry), the endocarp hard, 2-loculed or splitting into 2, 1-loculed pyrenes; seeds without endosperm.

A complex genus of about 244 specific and subspecific entities, mostly natives of subtropical and tropical America; a few also in tropical Asia and Africa; several are widely cultivated under hundreds of cultivar names. Interspecific hybridization is probably widespread in the genus.

a. Inflorescence conspicuously elongate and cylindric-spiciform, at least after anthesis.
  b. Stems usually appressed-pubescent or strigose.
    c. Leaves usually all ternate ..... 1. *L. trifolia*
    cc. Most or all the principal leaves decussate-opposite .... 1a. *L. trifolia* fo. *oppositifolia*
  bb. Stems conspicuously and densely spreading-hirsute.
    d. Leaf-blades thin-textured in drying, lightly puberulent beneath ..... 1b. *L. trifolia* fo. *hirsuta*
    dd. Leaf-blades heavy when dry, coarsely and conspicuously hirsute-hispid ..... 2. *L. maxima*
aa. Inflorescence capitate, not elongate-spiciform, flat or globose in age.
  e. Pubescence on stems glandular-capitate ..... 3. *L. glandulosissima*
  ee. Pubescence not noticeably glandular.
    f. Lowest bractlets much larger than the rest, conspicuous, ovate, often subinvolucrate.

g. Upper stems and foliage more or less densely velutinous or subvelutinous.
h. Corolla white ..... 4. *L. velutina*
hh. Corolla lilac, magenta, or violet ..... 4a. *L. velutina* fo. *violacea*
gg. Upper stems and foliage densely puberulent, pubescent, appressed-strigillose, or glabrescent.
i. Leaf-blades obtuse or rounded apically, pubescent beneath ..... 7. *L. involucrata* fo. *rubella*
ii. Leaf-blades sharply acute or acuminate apically, lightly strigillose or glabrescent beneath, revealing the densely resinous-punctate lamina.
j. Leaf-blades 7–12.5 cm long, the marginal teeth sparse, mostly triangular and sharply acute; bractlets narrowly elliptic, to 2 cm long ..... 8. *L. grosseserrata*
jj. Leaf-blades 1.5–8.5 cm long, the marginal teeth numerous, close together, mostly obtuse or rounded; bractlets ovate, less than 2 cm long.
k. Leaf-blades broadly ovate, coarsely serrate, the venation not conspicuously reticulate-bullate; lowermost bractlets broadly ovate, each more than 1 cm long ..... 9. *L. costaricensis*
kk. Leaf-blades narrowly lanceolate, ovate-oblong to ovate or elliptic, finely serrulate, the venation mostly conspicuously reticulate and more or less bullate; lowermost bractlets ovate, less than or to 1 cm long ..... 5. *L. hirta*
ff. Lowest bractlets not conspicuously larger than the rest nor broadly ovate.
l. Pubescence on well-developed stems, peduncles, and foliage densely long-hirsute, hispid, or setulose ..... 6. *L. hispida*
ll. Pubescence on stems, peduncles, and foliage neither long-hirsute nor setulose (or hispid-hirsute only on immature growth).
m. Pubescence on peduncles and branches densely short-hirsutulous; leaves usually densely puberulent or short-pubescent on both surfaces, especially beneath ..... 10. *L. moritziana*
mm. Pubescence on peduncles and branches minute and inconspicuous; leaves usually merely scabrellous above and sparsely scattered-pilosulous or strigillose beneath, sometimes glabrescent.
n. Stems and branches conspicuously prickly ..... 11b. *L. camara* var. *aculeata*
nn. Stems and branches mostly unarmed or with inconspicuous scattered prickles.
o. Young growth puberulent or short-pubescent ..... 11. *L. camara*
oo. Young growth densely spreading-hirsute ..... 11a. *L. camara* var. *mista*

1. **Lantana trifolia** L., Sp. Pl. 626. 1753.

Lippia purpurea Armano *ex* Dum. Cours., Bot. Cult., ed. 2. 7: 131. 1814.
Lantana pilosa H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 210. 1817.
L. celtidifolia H.B.K., loc. cit. 2: 210. 1817.
L. albo-purpurea Desf., Cat. Hort. Paris, ed. 3. 292. 1829.
Camara trifolia (L.) Kuntze, Rev. Gen. Pl. 1: 504. 1891.
C. trifolia var. *normalis* Kuntze, loc. cit. 1: 504. 1891.
Lantana trifolia var. *vulgata* Briq., Annuaire Conserv. Jard. Bot. Genève 7/8: 303. 1904.

Perennial *herbs* with woody underground stems or subshrubs to 2.5 m high; stems usually appressed-pubescent or strigose, the trichomes short and closely appressed or subappressed to the upper part of the stems. *Leaves* mostly ternate, usually membranous, oblong-lanceolate to elliptic-lanceolate or ovate, petiolate, 5–12 cm long, acute or acuminate apically, crenate-serrate, attenuate basally and decurrent into the petiole, often reticulate-rugose above and scabrous or more or less strigose-pubescent, densely resinous-punctate and scattered-puberulent or -strigillose beneath. *Inflorescences* spicate, subcapitate when young, later cylindric and elongating to 4.5 cm long, densely many-flowered; spikes at first subglobose, 1–1.5 cm in diameter; peduncles slender, usually shorter than or equaling the subtending leaves, 2–10.5 cm long, densely strigose-pubescent, solitary in each

leaf-axil; bractlets herbaceous, green, lanceolate or ovate, the lowest to 10 mm long and 3 mm wide, cuspidate-acuminate apically, 5-nerved, strigose above, loosely imbricate, the upper with the cusp about equaling the corolla-tube. *Flowers* with the corolla pink, lavender, lilac, or purple, the tube 5–6 mm long. *Drupes* fleshy, purple or lavender, 2–3 mm in diameter.

In hedges, thickets, and well-drained grasslands; widely distributed throughout tropical America from Mexico and Cuba to Argentina, Bolivia, and Peru; polymorphic and variable.

BOCAS DEL TORO: Almirante, along road to "Bomba," *Blum 1333* (MO). Bocas del Toro, *Carleton 148* (NY). Up the hill from "Bomba," W of Almirante, *Blum 1412* (MO). Edge of river and railway and adjacent rainforest, Changuinola and Teribe, 100–200 ft, *Lewis et al. 838* (LL). Vicinity of Chiriquí Lagoon, *von Wedel 1303* (MO). Isla Colón, *von Wedel 2962* (MO). Old Bank Island, *von Wedel 2072* (MO). Water Valley, *von Wedel 1643, 2659* (both MO). CANAL ZONE: Vicinity of Miraflores Lake, *White 146* (MO, NY). CHIRIQUÍ: Pastures and forested riverbanks E of Gualaca, 500 ft, *Allen 5037* (MO).

1a. **Lantana trifolia** fo. **oppositifolia** Moldenke, Phytologia 4: 179. 1953.

This form differs from the typical form of the species in having its principal leaves mostly decussate-opposite. It occurs sporadically almost throughout the range of the species.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1150* (MO). Macaw Hill, swamp at base of hills, *von Wedel 3* (MO, NY). PANAMÁ: Along Pan-Am Highway in open grazed area near Jenine, Río Cañita, *Duke 3848* (MO).

1b. **Lantana trifolia** fo. **hirsuta** Moldenke, Phytologia 3: 113. 1949.

This form differs from the typical form of the species in having its branches, branchlets, petioles, peduncles, and the upper portion of the stems spreading-hirsute or densely hirsute-pubescent, the trichomes longer than in the typical form. The leaf-blades are puberulent beneath.

The form occurs from Mexico and Cuba, through Central America and the West Indies, to Argentina, Bolivia, and Peru; also in the Hawaiian Islands and widely introduced in Indonesia, Hongkong, Ceylon, India, and Burma.

HERRERA: In open grassland and scrub, Ocú, *Ebinger 1080* (MO). PANAMÁ: Savannas along Panama National Highway, E of Panamá City, vicinity of Río Pacora, *Bartlett & Lasser 16470* (MICH). SAN BLAS: Ailigandi, *Dwyer 6846* (MO); Sasardi, 20 m, *Duke 10131* (BMIC).

2. **Lantana maxima** Hayek, Feddes Repert. 2: 164. 1906.

Herbaceous perennials or small, low, rounded bushes or shrubs, 0.5–2.6 m high, aromatic; stems and branches tetragonal, unarmed, densely spreading-villous, -hirsute, or -hispid, the branches divaricate. *Leaves* numerous, decussate-opposite, ternate, or quaternate, short-petiolate, the blades ovate or ovate-lanceolate, firm-textured and heavy when dry, 5–8 cm long and 3–4.5 cm wide, regularly serrate, acute apically, acuminate basally and prolonged into the petiole, usually conspicuously rugose-nervose, hirtellous or hirsute-hispid above, densely villous-tomentose beneath with canescent trichomes. *Inflorescences* axillary; heads at first ovate-globose, soon elongating and cylindric-spiciform, 2–5 cm long and ca. 1 cm wide; peduncles slender, 5–6 cm long, densely villous to hirsute-hispid;

bractlets conspicuous, ovate-lanceolate, 7–8 mm long and 2–3 mm wide, cuspidate-acuminate apically, densely appressed- or spreading-villous. *Flowers* with the corolla pink or rose to mauve, lavender, violet, lilac, or purple, yellowish-white basally, the tube ca. 8 mm long, narrow-cylindric, subpuberulent. *Drupes* fleshy, deep-pink, red, or magenta to purple or finally black.

On grassy plains and slopes, burned-over savannas, and coastal banks, in clearings of forests, brushy second-growth, and cultivated ground, and along canals and roadsides, in shade or in full exposure to the sun, from Trinidad and Panama throughout northern South America to Peru and Paraguay.

Known as "cariaquito morado," "maíz de zorro," "pajarito," and "venturosa."

This species is often difficult to distinguish from *Lantana trifolia* fo. *hirsuta*, but in *L. maxima* the pubescence is mostly long and rather shaggy, stiffy spreading at right angles over all or at least the upper parts of the plant, and the leaf-blades are characteristically densely hairy beneath. In the southernmost parts of its range in South America it merges into *L. fiebrigii* Hayek.

CHIRIQUÍ: Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1125* (NY). Llanos Francia, vicinity of Boquete, 3300 ft, *Stern et al. 1190* (MO, US). Tolé, *Tyson et al. 4231* (MO). COCLÉ: Road to El Cope from Pan American Highway, *Burch et al. 1386a* (MO). PANAMÁ: Second growth and culled forest on SE slope, Cerro Trinidad, *Kirkbride & Duke 1675* (US). SAN BLAS: Mainland Point opposite Isla Mosquito, *Duke 8984* (BMIC, MO).

3. **Lantana glandulosissima** Hayek, Feddes Repert. 2: 161. 1906.

L. crocea var. *guatemalensis* Loes., Verh. Bot. Vereins Prov. Brandenburg 53: 76. 1912.

Suffrutescent, 1–3.5 m high; stems to 2.5 cm in diameter, unarmed, smooth; branches and branchlets tetragonal, medullose, unarmed or with a few, small, weak, scattered, and inconspicuous prickles, more or less densely pilose or hirsute with long or short, wide-spreading, often canescent, stiff, and mostly gland-tipped trichomes, usually most densely hirsute with the longest, stiffest, and most conspicuously glandulose trichomes at the apex of the twigs. *Leaves* decussate-opposite, the blades chartaceous, ovate, with a faint watermelon odor when fresh, 2.3–14.5 cm long and 1–7.5 cm wide, acute or subacuminate apically, acute or abruptly acuminate basally and cuneately prolonged into the apex of the petiole, regularly crenate-serrate from almost the base to the apex with acute mostly small and rather appressed antrorse teeth, mostly slightly rugose-bullate above, scabrous and densely pilose-pubescent above (the trichomes sometimes all short and more or less antrorsely appressed, sometimes long and spreading, the longer mostly bulbous-based), mostly velutinous or tomentose beneath, sometimes merely short-pubescent or strigose-pubescent (densest along the larger venation), often glandular; petioles slender, 4–22 mm long, densely or sparsely spreading-hirsute or -pilose to more or less densely short-pubescent or puberulent, often glandular. *Heads* hemispheric, not elongating after anthesis, 1.5–2 cm wide; peduncles slender, firm, ascending, often more incrassate apically (especially in fruit), mostly subequaling or surpassing the subtending leaves, sometimes shorter, 2–14.5 cm long, densely spreading-hirsute with gland-tipped canescent trichomes to more sparsely pilose or even merely puberulent, mostly glandulose; bractlets not noticeable imbricate, narrow, linear-lanceolate or lanceolate to oblong, 3–7 mm long

and 0.8–2 mm wide, obtuse or acute apically, densely short-pubescent or strigose, the trichomes mostly canescent, appressed, and glandulose, sometimes spreading. *Flowers* with the corolla hypocrateriform, yellow or orange to red or vermillion, reddening in age and in drying, surpassing the bractlets, ca. 10 mm long, the tube short-pubescent. *Drupes* bluish to dark-purple or black, fleshy, edible.

Common on savannas and pine ridges, in forests, and along roadsides from northern Mexico to northern South America; also in Cuba and Puerto Rico; introduced in Nigeria; frequently cultivated elsewhere; almost certainly hybridizing with related species. In South America it merges into *Lantana glutinosa* Poepp.

CANAL ZONE: Locality unknown, *Krauss 223* (G). Ancon Hill, 600 ft, *Williams 13* (NY). Balboa Heights, *Greenman & Greenman 5025* (MO). Between Corozal and Ancón, 10–30 m, *Pittier 2178* (NY). At edge of forest between Chagres Batteries and Fort San Lorenzo, Fort Sherman, *Maxon & Valentine 6988* (NY). Vicinity of Monkey Hill, *Cowell 15* (NY). CHIRIQUÍ: Boquete, *Krauss 387* (MTMG). David, *Krauss 389* (MTMG). Occasional along weedy roadside, *Fosberg 27367* (NY). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1124* (NY). COCLÉ: Bismarck, *E. Wall*, 12 April 1928 (S). Above Penonomé, 2000–3000 ft, *Williams 534* (NY). Santa Clara, *Krauss 224* (G). Very common, hills S of El Valle de Antón, *Allen 2494* (US). DARIÉN: Trail between Cana and Boca de Cupe, vicinity of El Real, along road to Río Pirre, *Stern et al. 624* (BM). Río Chico, vicinity of Yaviza, 100 ft, *Allen 4581* (NY). PANAMÁ: Moist clearing, Old Experiment Station, 3 mi. E of Panamá, *Maxon et al. 7090* (NY). Old Panamá, *E. Wall 9* (GB). Panamá, *Hayes 758* (NY). Taboga Island, *Krauss 222* (G).

4. **Lantana velutina** Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(2): 325. 1844.

L. odorata var. *berlandieri* Torr. *in* Emory, U. S. Mex. Bound. Surv. 2: 128. 1859.
Camara velutina (Mart. & Gal.) Kuntze, Rev. Gen. Pl. 2: 504. 1891.
Lantana involucrata var. *velutina* (Mart. & Gal.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 172. 1936.

Small diffusely branched *shrubs*, to 2 m high, with an odor like rhubarb; stems unarmed, smooth; branches and branchlets slender, more or less densely short-pubescent or tomentose with spreading or subappressed trichomes, less so in age. *Leaves* decussate- opposite; the blades chartaceous, ovate or elliptic-ovate, 1–4 cm long and 7–28 mm wide, mostly acute or subacute apically, rarely short-acuminate or rounded, cuneately narrowed into the petiole basally, regularly crenate with small obtuse and antrorse teeth, mostly reticulate-rugose or bullate and densely pubescent or velutinous above, usually densely and softly canescent-tomentose or velutinous beneath; petioles slender, 1–9 mm long, densely tomentose, often winged. *Heads* hemispheric or slightly ovate-elongate in age; peduncles slender, 1–7.5 cm long, more or less densely short-pubescent with spreading or more rarely subappressed trichomes; bractlets large, conspicuous, membranous, closely imbricate, broadly ovate, the lowermost to 12 mm long and 8 mm wide, subacute or obtuse apically, broadly rounded and sessile, venose, densely appressed-pubescent or velutinous, shorter than the corolla or the lowermost equaling or even surpassing it. *Flowers* with the corolla hypocrateriform, usually white, often yellow in the throat, fragrant, the tube ca. 6 mm long, densely strigose-pubescent, the lobes densely strigose-pubescent outside but glabrate or only minutely appressed-puberulent within. *Drupes* fleshy, pink, sweet, edible.

In waste places, on mesas, slopes of foothills, alluvial plains, sandy bottoms, and llanos from southern Texas and northern Mexico to Venezuela; also on Socorro Island and sometimes cultivated.

CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo along Río Chiriquí Viejo, 1200 m, *Allen 973* (MO). PANAMÁ: Corozal to Pedro Miguel, *Cowell 411* (NY). Near beach at Nueva Gorgona, *Duke 4493* (UC).

This is a very polymorphic species; besides the following, other of the named forms and varieties are to be expected in Panama.

4a. **Lantana velutina** fo. **violacea** Moldenke, Phytologia 8: 161–162. 1962.

This form differs from the typical form of the species in having its corollas light-violet or light-purple in color, with a yellow center. It occurs sporadically throughout the range of the species.

PANAMÁ: Common in area of typical dry deciduous scrub, vicinity of Bejuco, *Allen 4513* (MO, NY, S).

5. **Lantana hirta** Grah., Edinburgh New Philos. Jour. 2: 186. 1826.

L. teucriifolia Otto & Dietr., Allg. Gartenzeitung 9: 371. 1841.
L. geroldiana Otto & Dietr., op. cit. 9: 372. 1841.

Bushes or slender shrubs, often leaning on other plants, 1–4 m high; stems 8–9 mm in diameter basally, covered with light-brown, rather shreddy, thin layers of bark, unarmed, the upper portions appressed-strigillose or glabrescent; branches many, opposite, the lower branches 6–7 cm from the ground. *Leaves* with a slight odor of cucumbers, normally decussate-opposite; the blades stiff, narrowly lanceolate or ovate-oblong to ovate or elliptic, 1.5–6 cm long and 1–3 cm wide, acute or acuminate apically, acute or obtuse basally, crenate, rugose and scabrous above, hispidulous-strigose along the venation beneath, varying to appressed-strigillose or even glabrescent; petioles short, slender. *Heads* 1–1.5 cm wide, not elongating or scarcely so in fruit; peduncles equaling or shorter than the subtending leaves; bractlets green, large, conspicuous, ovate to lanceolate or broadly ovate, the lower branchlets to 1 cm long and 8 mm wide, subinvolucrate. *Flowers* fragrant or disagreeably pungent; corolla hypocrateriform, mostly white with a pale-yellow center, sometimes pink or tinged with lavender, often becoming bluish in age, the tube ca. 7 mm long, the limb ca. 2 mm wide. *Drupes* dark-purple or black, fleshy, edible.

On dry hills and mountainsides, steep brushy or wooded pastured slopes, in pine or oak woods, fields, roadsides, banks, and thickets, Mexico to Panama; sometimes cultivated.

This species was confused with the next by Standley.

CHIRIQUÍ: Vicinity of Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 866* (MO, NY). Vicinity of Boquete, 1000–1300 m, *Maxon 5137* (NY). Lumber road into hills E of Río Caldera, 4500–6500 ft, *Allen 4659* (MO, NY). Vicinity of Finca Lérida, 1750 m, *Woodson & Schery 216* (MO). Common in burned areas, forested ridges S of Finca Lérida, 6000–7000 ft, *Allen 4762* (MO, NY). Finca Lérida to El Boquete, 1300–1700 m, *Woodson et al. 1123* (NY). Lava field north of town of Volcán, ca. 4600 ft, *Duke 9148* (BMIC, MO).

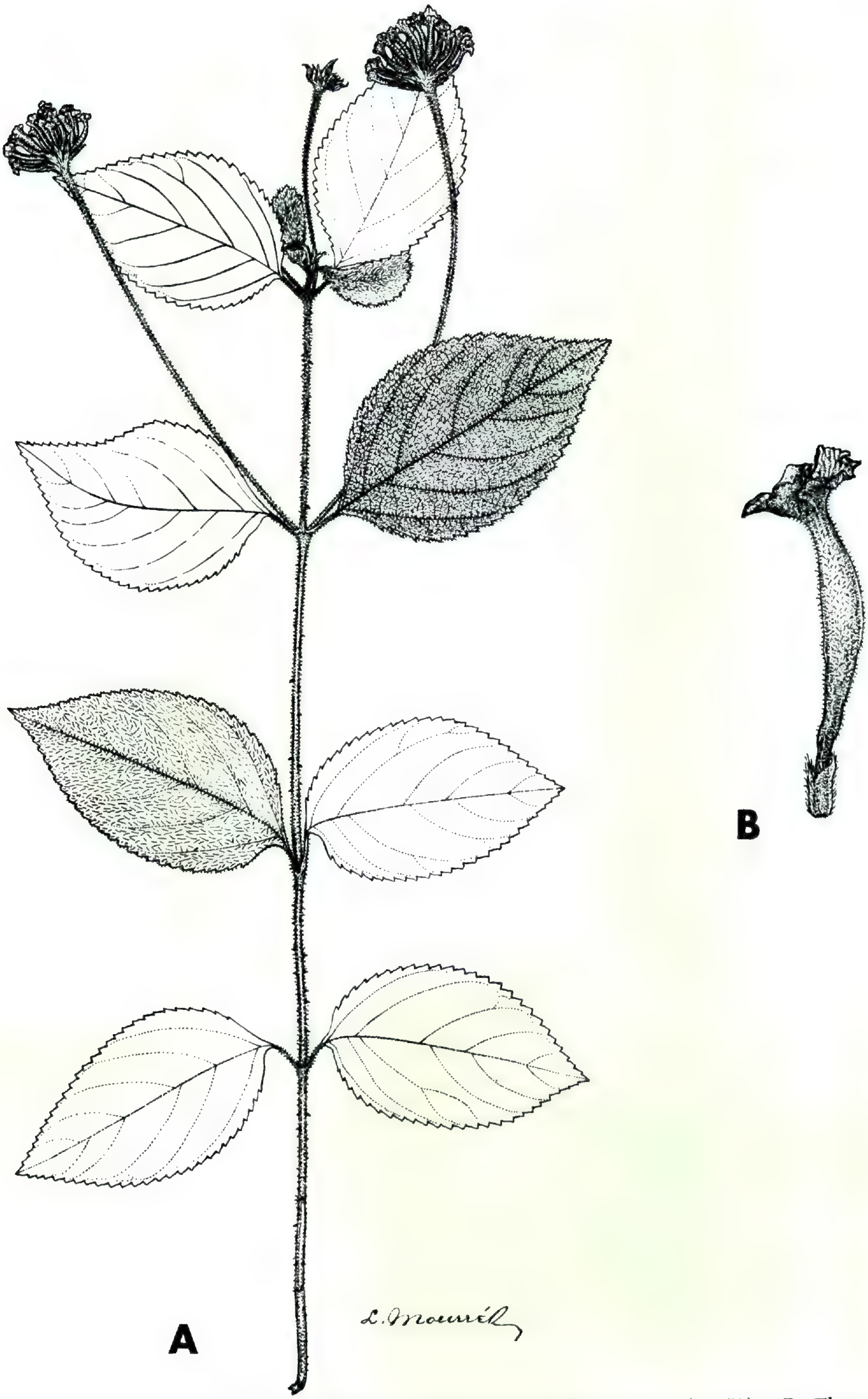

FIGURE 2. *Lantana hispida* H.B.K.—A. Habit with inflorescences (× 5/7).—B. Flower (4⅓). [After *Allen 971* (MO).]

6. **Lantana hispida** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 211. 1817.—FIG. 2.

L. hirsuta Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(2): 326. 1844.
L. polyacantha Schau. *in* A. DC., Prodr. 11: 597. 1847.

Subshrubs or irregular shrubs, 0.3–3.2 m high, spreading, often semi-scandent; stems tetragonal, unarmed or slightly thorny, usually densely scabrid-hirtous or hispid, usually densely hispid on the younger parts. *Leaves* decussate-opposite; the blades thin-chartaceous or membranous, broadly ovate, 5–7.5 cm long and 2.2–6 cm wide, acute or acuminate apically, rounded basally, regularly crenate or crenulate, often somewhat cuneately attenuate into the petiole at the center, pilose-hispid with abundant bulbous-based trichomes above, rough-hirsute beneath, densely hirsute-hispid on both surfaces when young, petioles 1.3–2 cm long, usually more or less densely hirsute-hispid. *Heads* hemispheric, flat, 1.5–2 cm wide, densely-flowered, not elongating after anthesis; peduncles hirtous or hispid, shorter than or equaling to surpassing the subtending leaves, usually more or less densely hirsute-hispid; bractlets lanceolate, shorter than the corollas, to 5 mm long and 1.5 mm wide, hirsute or hirsutulous. *Flowers* with the corolla hypocrateriform, opening yellow, turning to orange, red, or scarlet in age. *Drupes* fleshy, blue.

In open pastures and thickets, along roadsides, on shrubby or forested slopes of hillsides, in pinewoods, llanos, and the edges of forest clearings, Mexico to Venezuela.

Apparently quite variable or perhaps consisting of several entities as here interpreted, some of which are very close to *Lantana tiliaefolia* Cham.

BOCAS DEL TORO: Up the hill from "Bomba," W of Almirante, *Blum 1413* (MO). Bocas del Toro, *von Wedel 187* (MO). CANAL ZONE: Barro Colorado Island, open sunny areas, *Ebinger 29* (MO). Near boat landing, *Stoutamire 2040* (MICH). Roadbank in sun, near Survival School, Curundu, *Tyson 1066* (MO). Vicinity of former town of Empire, Culebra Cut and vicinity, *Hunter & Allen 771* (MO, NY). Vicinity of France Field, *Blum & Dwyer 2119* (MO). In government forest along Las Cruces Trail, 75 m, *Hunter & Allen 746* (MO). Open sunny areas, Corrosion Laboratory, Miraflores Locks, *Stern et al. 71* (BM, MO). CHIRIQUÍ: In second growth, cultivated areas, and roadsides, from Boquete to 3 mi. N, 3300–4200 ft, *Lewis et al. 616* (LL). Llanos Francia, vicinity of Boquete, 3300 m, *Stern et al. 1159* (BM, MO). Common, roadbanks and brushy areas, Río Macho de Monte, 1 mi. E of Cuesta de Piedra, 2800 ft, *E. L. Tyson 897* (MO). Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1200 m, *Allen 971* (MO). COLÓN: On sandy beach, Piña, *A. R. Moldenke 1225* (AAU). DARIÉN: Road from El Real to Pinogana, *Duke 4889* (LL). LOS SANTOS: Savanna vegetation, 3 mi. S of La Palma, *Correa A. & Gallegos 75* (MO). SAN BLAS: From secondary growth around cemetery near Mulatupu, up Río Ibedi, *Duke 8491* (BMIC). Soskatupu Island, on the only hill on the island, 150 ft, *Kirkbride 183* (MO). VERAGUAS: 2 mi. W of Santiago on Pan American Highway, *Dwyer et al. 7554* (MO).

Known as "nicedudo" or "Nicetutu" (fide *Duke 8491*).

7. **Lantana involucrata** fo. **rubella** Moldenke, Phytologia 14: 325. 1967.

Pubescent, much-branched *shrubs*, 0.6–1.5 m high, or occasionally small trees to 4 m; branches stiff, spreading, tetragonal or nearly terete, the bark commonly fissured. *Leaves* with the blades elliptic or ovate, varying to oblong, lanceolate, obovate, or even rhomboid-subrotund, petiolate, 1–4 cm long and 25 mm wide, blunt or obtuse to rounded apically, narrowed or obtuse basally or cuneately

prolonged into the petiole, uniformly crenulate with rounded appressed teeth from the apex almost to the base, reticulate-rugose and more or less scabrous above, short-pubescent beneath. *Heads* globose, dense, several- to many-flowered, inconspicuously involucrate; peduncles usually surpassing the leaves, slender, 1–5 cm long, strigose, usually canescent; outer bractlets broadly ovate or ovate-lanceolate, 3–6 mm long and 2–5 mm wide, sericeous-strigose, acute, equaling the flowers, inner bractlets much smaller, ovate-subrotund, subacuminate, half as long as the flowers. *Flowers* with the corolla pink or lilac to mauve or violet, the throat yellowish, the tube 2–8 mm long. *Drupes* fleshy, blue, 3–4 mm in diameter.

Open places, sandy plains, and beaches, occasional with the typical white-flowered form of the species in Florida, Hispaniola, and probably other parts of the Caribbean area.

SAN BLAS: Sunset Island, Isla Mosquito, *Duke* 8875 (MO).

8. **Lantana grosseserrata** Moldenke, Phytologia 1: 420. 1940.

Straggling *shrubs* to 2.5 m high; branchlets slender, acutely tetragonal, sparsely or densely appressed-strigose with yellowish trichomes. *Leaves* decussate-opposite, the blades chartaceous, slightly lighter green beneath, elliptic, 7–12.5 cm long and 2.8–4.8 cm wide, attenuate-acuminate basally and apically, coarsely and irregularly serrate-dentate from about the middle to the apex with mostly 7–10 sharply acute broadly triangular and divergent teeth on each side, sparsely and minutely pilosulous above, densely resinous-punctate beneath and sparsely short-pilosulous on the venation beneath; petioles 5–7 mm long, densely short-pubescent with substrigose trichomes. *Inflorescences* axillary, long-pedunculate, capitate; peduncles slender, 6.5–7.5 cm long, sparsely strigose; bractlets numerous, conspicuous, narrowly elliptic, 6–20 mm long and 2–4 mm wide, densely resinous-punctate, venose, appressed-strigillose on the venation, acute. *Flowers* with the corolla white, the tube ca. 6 mm long, the limb ca. 2 mm wide. *Drupes* black, fleshy.

In bushy clearings, Costa Rica and Panama.

COCLÉ: Bismarck, above Penonomé, 2000–3000 ft, *Williams* 545 (NY, US).

9. **Lantana costaricensis** Hayek, Feddes Repert. 2: 162. 1906.

Shrubs, to 2 m high; stems many, basal, slender, arching, obtusely tetragonal, unarmed, brown in drying, abundantly short-pubescent with stiff partially spreading trichomes; branches unarmed, virgate, subterete, sparsely setose; nodes not ampliate. *Leaves* decussate-opposite, the lower often with much abbreviated twigs in their axils, the blades membranous or thinly chartaceous, ovate or ovate-lanceolate, dark-green above, lighter beneath, 3.5–8.5 cm long and 1.5–4 cm wide, mostly acute or sometimes short-acuminate or cuspidate-acuminate apically, short- or long-attenuate into the petiole basally, crenate-serrate from below the widest point to the apex, the teeth acutish or obtuse, somewhat scabrellous or even scabrous above, rough-setulose with bulbous-based trichomes and more or less scattered-pilose or -puberulous, densely resinous-punctate beneath, subglabrate on the lamina, but sparsely or more or less densely appressed-pilose on the venation; petioles not distinct, 5–8 mm long, densely subantrorsely pubescent or

setose-hispid. *Inflorescences* equaling or slightly surpassing the subtending leaves, the heads capitate, flat during anthesis, 1.5–2 cm wide, conspicuously bracteate, somewhat elongating to 2.5 cm in fruit; peduncles slender, ascending, densely pubescent with antrorsely spreading or setose trichomes; bractlets foliaceous, ovate, the basal branchlets 8–15 mm long and 5–6 mm wide, attenuate-acuminate, about twice as long as the flowers, densely resinous-glandular and scattered-pilose or hispidulous, the inner acuminate and about equaling the corolla-tube. *Flowers* with the corolla white or pale lavender, with a chrome-yellow center, 5–7 mm long, puberulent and glandular-punctate.

On riverbanks, in forest clearings, and at the edges of cultivated land, Mexico to Panama.

CHIRIQUÍ: At edge of coffee plantation, Fred Collins Finca, Boquete, 6000 ft, *Ebinger 658* (MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2440* (MO).

10. **Lantana moritziana** Otto & Dietr., Allg. Gartenzeitung 9: 369–370. 1841.

Bushes or large shrubs, 1–5 m high, spreading and semi-scandent or sometimes robust and tree-like, with an unpleasant odor; stems tetragonal, usually spiny; branches herbaceous, obtusely tetragonal, often unarmed, usually densely short-pubescent or short-hirsutulous throughout, more conspicuously so on the younger portions, the trichomes mostly non-glanduliferous. *Leaves* decussate-opposite or rarely ternate, the blades membranous, ovate, 2.5–10.5 cm long and 1.8–8 cm wide, mostly acute or short-acuminate apically, abruptly cuneate-acuminate basally, regularly crenate-serrate or serrulate from the start of the basal acumination to the apex with numerous mostly appressed or subappressed rounded teeth, densely puberulent or antrorsely appressed-pubescent above, glabrate in age, much more densely and persistently pubescent beneath; petioles slender, 0.5–2.7 cm long, densely short-pubescent. *Inflorescences* axillary, usually equaling or surpassing the subtending leaves, the heads hemispheric, 1.5–2 cm wide, densely many-flowered, not elongating in age; peduncles slender, 4–10 cm long, densely short-hirsutulous; outer bractlets often conspicuous, lanceolate, 5–7 mm long and 1–2 mm wide, acute, densely strigillose-pubescent, the inner smaller. *Flowers* odorous; corolla various shades of yellow, orange, and red, usually opening yellow or yellowish-orange and changing to orange-red, red, or pink, finally pale-crimson, carmine, vermillion, lavender-pink, purple, violet, plum-color, or reddish-brown, the tube slender, ca. 9 mm long. *Drupes* fleshy, blue or purple, finally black.

In various habitats, including forest edges and clearings, thickets, fencerows, pastures, open woods, rocky xerophytic slopes, marshy land, beaches, and cultivated ground, Mexico to Peru and southern Brazil.

Vernacular names are "cariaquito," "casarachico-sacha," "chumbinho," "escoba," "flor de sangre," "murupacha," "ramoncillo," and "venturosa." In northern South America an extract of the leaves is used to make a tea to alleviate stomach-ache, catarrh, and whooping-cough, or just as a cold drink. This species has been widely confused with *Lantana camara*, which it greatly resembles.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1117* (MO). Shepherd Island, *von Wedel 2733* (MO). Banks of river and adjacent rainforest, 10–15 mi. inland S from mouth of Río Changuinola, *Lewis et al. 898* (LL). CANAL ZONE: United States Army Tropic Test

Center Site, Albrook AFB, *Dwyer & Robyns 120* (MO). Ancon Hill, *Duke 4607* (MO, UC). Rainforest, SE of Kobbe Beach, Howard Air Force Base, *Oliver & MacBryde 1898* (MO). Roadside woods along Panamerican Highway between Rodman Marine and Chorrera, *Nowicke et al. 3590* (LL). Sosa Hill, *Duke 4667* (MO, UC). CHIRIQUÍ: Finca Lérida to Boquete, ca. 1300–1700 m, *Woodson et al. 1124* (MO). COCLÉ: Río Hato airstrip, *Burch et al. 1141* (LL, US). COLÓN: Secondary forest, Santa Rita Ridge, ca. 3 mi. E of Transisthmian Highway, *Lewis et al. 5371* (LL). HERRERA: In open pasture, 0.5 mi. NE of Ocú, *Stern et al. 1708* (MO, US). PANAMÁ: Edge of river and cloud forest, Altos del Río Pacora, 2500 ft, *Lewis et al. 2341* (MO). Savannas near Chepo, 30 m, *Hunter & Allen* 35 (MO). In open grazed area near Jenine, Río Canita, *Duke 2813* (AAU). In open pasture land, playa near Ríomar, *Ebinger 509* (MO). Roadside savanna between Río Pacora and Chepo, *Dwyer et al. 5095* (AAU).

11. **Lantana camara** L., Sp. Pl. 627. 1753.

L. mutabilis Weigel, Physiogr. Sälsk. Handl. 1: 46. 1776.
L. scabrida Soland. *in* Ait., Hort. Kew., ed. 1. 2: 352. 1789.
L. antillana Raf., Sylv. Tellur. 82. 1838.
Camara vulgaris Benth., Bot. Voy. Sulphur 154. 1846.
Lantana mexicana Turner, Flor. Kingd. 181. 1876.
Camara aculeata var. *subinermis* Kuntze, Rev. Gen. Pl. 1: 503. 1891.

Branching *shrubs*, to 2 m high; stems and branches mostly unarmed or slightly prickly, usually minutely and inconspicuously pubescent. *Leaves* decussate-opposite; the blades chartaceous, ovate to oblong-ovate, 2–12 cm long and 2–4.5 cm wide, acute or short-acuminate (rarely obtuse apically), acutely narrowed or abruptly rounded to a subcuneate acumination basally, crenate-serrate, more or less reticulate-rugose and decidedly scabrous or scabrellous above, usually only sparsely pilosulous or strigillose beneath (mostly only on the venation) with canescent or brownish trichomes, sometimes glabrescent; petioles 7–12 mm long. *Inflorescences* axillary, shorter than, equaling, or surpassing the subtending leaves, the heads always capitate, hemispheric, to 3 cm wide, not elongating after anthesis, many-flowered; peduncles slender, 2–9 cm long, more or less appressed-pilose or puberulent; bractlets usually not conspicuous, oblong to lanceolate, equal, 4–7 mm long, and 1–1.5 mm wide, subulate or acute, rarely a few larger ones also present, appressed strigose-pubescent, usually about as long as the corolla-tube. *Flowers* with the calyx thin, ca. 3 mm long; corolla hypocrateriform, mostly orange-yellow or orange, changing to red or scarlet in age, the tube ca. 10 mm long, barely enlarged above the middle, slightly curved, puberulent, the limb 6–8 mm wide. *Drupes* fleshy, black, ca. 3 mm in diameter.

Hillsides, woods, thickets, hedges, fencerows, and waste places, widely distributed in tropical and subtropical America from Florida through the West Indies and South America to Argentina, Bolivia, and Peru; less common in its typical form in Central America; introduced and naturalized in the tropics and subtropics [mostly as var. *aculeata* (L.) Moldenke] of the Old World where it has become a troublesome weed in some places; widely cultivated in hundreds of cultivars; probably originally West Indian, but now widely misinterpreted.

Among its 150 recorded vernacular names are "bandera español," "camará," "camará vermelho," "cambara verdadeiro," "chichiquelite," "cinco negritos," "confituria," "coronitas," "dame cubre galanos," "English sagebush," "filigrana," "flor de duenda," "flor de sangre," "guripacha," "herva de lagarto," "jaral," "jarilla," "malmequer do campo," "more de caballo," "red sagebush," "sangre linda,"

"señorita," "siete colores," "sotarre," "tickberry," "tres colores," "venturosa," "wild sage," and "yerba mora."

A quinine-like alkaloid, lantanine, occurs in this plant and is used medicinally as an antispasmodic; a toxic substance, lantadene, causes "pink-nose," a photosensitivity disease in cattle and sheep. The powdered roots in milk are given to children in the treatment of colic and stomach-ache; an infusion of the whole plant is used for catarrh and bronchitis; a leaf decoction is used for constipation, as a febrifuge and diaphoretic, externally for ophthalmia and festering sores, and in baths and hot fomentations for dropsy. In Colombia the plant is used as an emenagogue and diaphoretic and in Brazil in baths as an anti-rheumatic.

CANAL ZONE: Arraijan, *Porterfield*, 26 Dec. 1933 (NY). Old Panamá, *Porterfield*, 30 Dec. 1933 (NY). Summit, *Krauss 707* (UC). COLÓN: Very common 0.6 mi. from Gatuncillo on Transisthmian Highway, *Correa A. 65* (MO). PANAMÁ: In woods along PanAm Highway about half-way between El Llano and Río Mamoní, *Duke 5570* (AAU). SAN BLAS: Permé, *Cooper 263* (NY).

11a. **Lantana camara** var. **mista** (L.) L. H. Bailey, Cycl. Amer. Hort. 884. 1900.

L. mista L., Syst. Veg., ed. 12. 417. 1767.
L. mixta Medic., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 3, Phys. 227. 1775.
L. coccinea Lodd. *ex* G. Don *in* Loud., Hort. Brit. 245. 1830.
L. mutabilis Lippold *ex* Otto & Dietr., Gartenzeit. 10: 314. 1842.
Camara aculeata var. *subinermis* fo. *mista* (L.) Kuntze, Rev. Gen. Pl. 1: 503. 1891.
C. aculeata var. *normalis* fo. *mista* (L.) Kuntze, loc. cit. 1: 503. 1891.

This variety differs from the typical form of the species in having its youngest growth densely spreading-hirsute, rather than appressed-puberulent.

Its distribution is about the same as that of the typical form of the species. Other varieties are to be expected in Panama, *e.g.* var. *nivea* (Vent.) L. H. Bailey (with the flowers opening white, changing to bluish in age, the stems coarsely armed), var. *flava* (Medic.) Moldenke (with the flowers opening bright-yellow, changing to saffron; the stems mostly unarmed), var. *mutabilis* (Hook.) L. H. Bailey (with the flowers opening white, then turning yellow, and finally rose or lilac), var. *sanguinea* (Medic.) L. H. Bailey (with the flowers opening saffron and turning bright-red), var. *alba* Moldenke (opening flowers with the tube yellow and the limb white, in age completely white; the stems unarmed), etc.

COLÓN: Colón, *Krauss* 388 (MTMG). PANAMÁ: Woods along Pan American Highway between El Llano and Río Mamoní, *Duke 5574* (LL). Taboga Island, *Krauss 706* (UC).

11b. **Lantana camara** var. **aculeata** (L.) Moldenke, Torreya 34: 9. 1934.

L. aculeata L., Sp. Pl., ed. 1. 627. 1753.
Camara aculeata (L.) Kuntze, Rev. Gen. Pl. 1: 503. 1891.
C. aculeata var. *normalis* Kuntze, loc. cit. 1: 503. 1891.
Lantana spinosa L. *ex* Le Cointe, Amaz. Bras. III Arvor. & Pl. Uteis 83. 1934.

This variety differs from the typical form of the species in having the branches and branchlets conspicuously prickly.

The variety is widespread throughout subtropical and tropical America from Florida and Mexico to northern Argentina; naturalized and often a serious pest in many parts of southern Europe, Africa, Madagascar, Asia, the islands of the Pacific, and Australia.

PANAMÁ: Taboga Island, *Née 147* (MA).

3. PHYLA

Phyla Lour., Fl. Cochinch., ed. 1. 66. 1790.

Zapania Scop. *ex* A. L. Juss., Ann. Mus. Natl. Hist. Nat. 7: 72. 1806.
Platonia Raf., Med. Repos. 5: 352. 1808.
Diototheca Raf., Fl. Ludov. 74. 1817.
Bertolonia Raf., Amer. Monthly Mag. & Crit. Rev. 2: 267. 1818.
Blairia Gaertn. apud Steud., Nom. Bot., ed. 1. 111. 1821.
Piarimula Raf., Fl. Tellur. 2: 102. 1836.
Pilopus Raf., loc. cit. 2: 102. 1836.
Panope Raf., loc. cit. 2: 103. 1836.
Cryptocalyx Benth., Ann. Nat. Hist., Ser. 1. 2: 446. 1839.

Perennial mostly procumbent or creeping *herbs*, stems trailing or ascending, sometimes slightly woody basally, more or less incanous throughout with appressed-strigose, rarely subglabrous malpighian (medifixed) trichomes. *Leaves* decussate-opposite, often fleshy, flat or pinnately plicatulate. *Inflorescences* spicate, axillary, cylindric, densely many-flowered, usually greatly elongate in fruit, solitary, paired, or ternate, never aggregated into corymbs or panicles. *Flowers* small, sessile, borne singly in the axils of small cuneate-obovate or flabelliform bractlets, not at all 4-ranked; calyx small, membranous, ovoid-campanulate or compressed and 2-carinate or winged, the rim 2- or 4-fid or 4-dentate; corolla irregular, the tube straight or incurved, slender, slightly exserted from the calyx, equal in diameter throughout or slightly ampliate above, the limb oblique, spreading, somewhat 2-lipped, 4-parted, the lobes broad, often retuse apically, the posterior entire, emarginate, or bifid to about the middle, the laterals exterior, the anterior often larger; stamens 4, didynamous, included or slightly exserted, the anthers unappendaged; ovary 2-loculed, the ovules 1 per locule, the stigma incrassate, oblique or recurved. *Fruit* small, dry, included by the calyx and sometimes adnate to it, dividing into 2 pyrenes at maturity, the pericarp leathery and hard, the exocarp membranous and rarely distinct from the pyrenes.

A difficult genus of about 20 species and subspecific entities, widely distributed in subtropical and tropical America, with one or two in the warmer parts of the Old World. Some forms are widely cultivated for lawns or as soil-binders.

a. Peduncles usually much shorter than the flowering spikes; spikes often 4 or more at each node ---------- 1. *P. betulaefolia*
aa. Peduncles usually much longer than the flowering spikes; spikes 1 or 2 at a node.
  b. Leaf-blades widest below the middle, mostly ovate or oval.
    c. Stems woody basally; trichomes on upper leaf-surface bulbous-based; leaf-blades mostly scabrous above, plainly acute apically ---------- 2. *P. scaberrima*
    cc. Stems herbaceous throughout; trichomes on upper leaf-surface appressed-strigose, not bulbous-based; leaf-blades not scabrous above, mostly obtuse apically.
      d. Mature leaves mostly to 7.5 cm long and 2 cm wide ---------- 3. *P. strigulosa* var. *strigulosa*
      dd. Mature leaves mostly less than 1.5 cm long and to 1 cm wide ---------- 3a. *P. strigulosa* var. *sericea*
  bb. Leaf-blades widest above the middle, mostly cuneate-obovate, spatulate, or narrowly oblanceolate.
    e. Leaves uniformly narrow-elongate, to 5.5 cm long and 4–10 mm wide ---------- 4a. *P. nodiflora* var. *longifolia*
    ee. Leaves cuneate-spatulate, spatulate, obovate, or rhomboid, mostly 1–3 cm long.
      f. Teeth on leaf-blades mostly large and coarse, more or less conspicuously divergent ---------- 5. *P. incisa*

ff. Teeth on leaf-blades mostly small and antrorsely appressed, usually not conspicuously divergent ..... 4. *P. nodiflora* var. *nodiflora*

1. **Phyla betulaefolia** (H.B.K.) Greene, Pittonia 4: 48. 1899.

Lippia betulaefolia H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 214. 1817.
Cryptocalyx nepetaefolia Benth., Ann. Nat. Hist., Sér. 1. 2: 446. 1839.

Sprawling *herbs*, with procumbent, often hollow stems rooting at the nodes, and ascending branches; stems and branches tetragonal when fresh, more or less appressed-strigose or strigillose with elongate whitish trichomes. *Leaves* with the blades thin-chartaceous or submembranous, rhomboid-ovate or ovate, often decidedly plicate, 1.5–8 cm long and 1.5–4.7 cm wide, acute apically, cuneately attenuate into the petiole basally, coarsely serrate-dentate (except on the basal cuneate acumination) with sharply acute or subacuminate teeth, densely or sparingly appressed-strigose with elongate whitish trichomes on both surfaces; midrib and secondaries impressed above, prominent beneath; petioles slender, 4–30 mm long, strigose like the branches or sometimes more densely villous with spreading elongate whitish trichomes. *Spikes* densely many-flowered, at first ovate-capitate, later elongate-oblong, to 1.5 cm long; peduncles varying from solitary in the leaf-axils to paired or in 3's, 2–6 or more per node, mostly greatly abbreviated, 1–4 mm long, shorter than the flower-spikes, and than the subtending petioles, rarely elongate to 2.8 cm; bractlets membranous, ciliate, cuneate from the dilated apex, abruptly cuspidate, the cusp slightly surpassing the corollas. *Flowers* numerous, tiny, closely imbricate in many ranks; calyx less than 1 mm long; corolla pale-pink or pale-purple, varying to white, ca. 1 mm long. $2n = 36$.

In low wet or swampy ground and open brush, woods, meadows, savannas, pastures, desiccated pools, and cleared land, from Cuba, British Honduras, and Guatemala to Brazil and Paraguay.

It is known as "filigrana," "herva cidreira brava," "malva de laguna," "malva rosa do campo," "manzanilla," and "tambu." In Brazil the leaves are used for making a drink.

CANAL ZONE: Ditch bank, edge of forest, Margarita Swamp, S of France Field, *Valentine 7068* (US). COLÓN: Sea level, Fató, Nombre de Díos, *Pittier 4144* (US). PANAMÁ: Vicinity of La Jagua, wet savanna area east of Panamá, *Bartlett & Lasser 16371* (MICH). Panamá, *Neé 94* (MA).

2. **Phyla scaberrima** (A. L. Juss.) Moldenke, Feddes Repert. 41: 64. 1936.

Zapania scaberrima A. L. Juss. *ex* Pers., Syn. Pl. 2: 140. 1807.
Lippia dulcis Trev., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13(1): 187. 1826.
L. dulcis var. *mexicana* Wehmer, Pflanzenst. 646. 1911.
L. mexicana Grieve, Modern Herb. 2: 831. 1931.
Phyla dulcis (Trev.) Moldenke, Torreya 34: 9. 1934.

Usually *shrubby* (at least basally) and erect, 0.3–1.5 m high, usually less than 60 cm, sometimes herbaceous and procumbent, perennial, decidedly aromatic, sometimes semi-aquatic; main stems mostly woody and erect, sometimes diffuse, long and trailing; branches mostly procumbent or ascending, often rooting at the nodes, subterete, often purplish, strigose-puberulent or strigillose with canescent trichomes. *Leaves* with the blades membranous, rhombic-deltoid, broadly ovate,

or oblong-ovate, 2–5 cm long and 7–10 mm wide, mostly acute or acuminate (rarely obtuse) apically, abruptly and shortly cuneate-narrowed into the petiole basally, coarsely crenate-serrate, substrigose above with stiff bulbous-based trichomes which soon break off, the bulbous bases persistent and rendering the leaf-surface decidedly scabrous, sparsely or densely strigillose or substrigose-pubescent with very short trichomes beneath and glandular-pulverulent; petioles 5–18 mm long, strigillose. *Spikes* ovate-globose when young, later cylindric and greatly elongating, 5–6 mm in diameter, eventually to 3.1 cm long, densely many-flowered, mostly equaling or shorter than the subtending leaves, often flexuous when elongate; peduncles solitary in the leaf-axils, not more than 2 per node, 1.5–4 cm long, densely short-pubescent or strigillose, much longer than the flowering spikes; bractlets membranous, closely imbricate, cuneate-obovate, obtusely and abruptly acuminate, strigose-hirtellous, ciliate, equaling the corollas. *Flowers* with the calyx small, bifid, villous, corolla white, 1–1.5 mm long, the limb exiguous, the lobes erect.

In fields, clearings, waste places, wet or muddy ground, llanos, pine woods, riverbanks and shady roadsides, from Cuba and Mexico through Central America to Panama and Venezuela.

Among its numerous vernacular names are "corronchocho," "cuacilaca," "dulce pungente," "hierba buena," "hierba dulce," "hoja dulce," "injerto," "malba," "orosul," "orosus," "orozus de monte," "orozuz," "orozuz de la tierra," "orozuz del país," "salvia americana," "salvia santa," "secapalo," and "yerba dulce."

Used pharmaceutically under the name "lippiae mexicanae" for diseases of the respiratory organs, chronic bronchitis, asthma, and related ailments, it contains volatile oils, lippiol, tannin, and menthol. In Central America this species is used as a haemostatic agent; in Cuba and South America as a pectoral in the treatment of coughs, colds, and chest ailments. In Mexico children enjoy eating the fresh leaves.

CANAL ZONE: Culebra, *Cowell 216* (NY). CHIRIQUÍ: Bouquete, 5500 ft, *Dwyer 7016* (MO). PANAMÁ: Panamá, *Seemann s.n.* (GH).

3. **Phyla strigulosa** (Mart. & Gal.) Moldenke, Phytologia 2: 233. 1947. var. **strigulosa.**

Lippia strigulosa Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles, Sér. 1. 11(2): 219. 1844.
L. nodiflora δ umbrosa Walp., Repert. Bot. Syst. 4: 49. 1845.
Phyla yucatana Moldenke, Phytologia 2: 140. 1948.

Procumbent *herbs*, freely branched from the base; branches slender, rooting at the nodes, obtusely and irregularly tetragonal, often deeply and irregularly sulcate, often reddish or purplish basally, canescent-strigillose with closely appressed antrorse trichomes, the tips ascending or erect; secondary branches more slender, stramineous, erect. *Leaves* numerous; the blades ovate or ovate-elliptic, mostly conspicuously widest below the middle, uniformly green on both surfaces, 1.5–8 cm long and 0.5–4.5 cm wide, rounded or acute apically, acuminate basally and prolonged into the petiole, conspicuously and regularly dentate with sharply acute or apiculate, broadly triangular, divergent teeth from the apex to the widest part, the margins of the teeth thick and often more or less involute, both surfaces

densely canescent-strigillose with short, closely appressed trichomes, the midrib slender, plane above, strong and prominent beneath, the secondaries slender, 4–6 per side, plane above, strong and prominent beneath, extending conspicuously to the leaf-margins and ending in the sinus between 2 teeth, often with 1 or 2 short branches issuing almost at the apex and extending to the apiculation of the nearest tooth; petioles 1–5 mm long, mostly winged and merging apically into the blade, obscurely canescent-strigillose or becoming glabrescent. *Inflorescences* axillary, capitate, the heads densely many-flowered, 4–8 mm long, elongating to 1.5 cm in fruit; peduncles slender, 2.5–5.5 cm long, usually only 1 per node, deeply sulcate, densely canescent-strigillose or glabrescent; bractlets ovate or broadly elliptic, ca. 3 mm long and 1.5 mm wide, sharply acute or long-acuminate, densely canescent-strigose, strongly costate. *Flowers* with the calyx minute; corolla pale pink, pale-lavender, lilac-pink, bluish, or purple to white, often with a rose-purple "eye," ca. 3 mm long, the limb ca. 1.5 mm wide. $n = 18$.

Often very common in clay or limestone soil in woods and copses, fields, marshes, swamps, and ditches, in muddy hollows, mud lakes, and along streams, in open ground, waste places, and along roadsides, from southern Texas and most of Mexico, through Central America, and from Cuba and the Dominican Republic, through the West Indies to Bolivia and Paraguay; also on the Galapagos Islands.

It is known as "fog fruit," "hierba dulce," "turre hembra," and "yerba de sapo." *Verbena fruticosa* Mill. is sometimes cited as a synonym of this plant and, if this were correct, its specific epithet would have to be adopted. However, Miller's name appears to be based on a mixture. Examination of a photograph of what is probably the type collection in the herbarium of the British Museum shows it to consist of three separate stems, two of which are *Phyla nodiflora* var. *reptans* (H.B.K.) Moldenke and the third is *P. strigulosa*. All were grown in the Chelsea Physick Garden from seed sent by William Houstoun from Campeche, Mexico. Because it is based on a mixture, the name could be interpreted as applying to either of the two elements. I have chosen to apply it to the two stems of *P. nodiflora* var. *reptans*.

Lippia queretarensis H.B.K. has also been suggested as being conspecific with *Phyla strigulosa*. If so, then its specific epithet will have to be employed. The original description, however, does not agree with this plant in leaf shape. Therefore, until the type or a photograph thereof is available to me, I am not making the transfer.

PANAMÁ: Panamá, *Neé 81* (MA).

3a. **Phyla strigulosa** var. **sericea** (Kuntze) Moldenke, Phytologia 19: 435. 1970.

Lippia nodiflora α *normalis* fo. *sericea* Kuntze, Rev. Gen. Pl. 2: 508. 1891.
L. nodiflora α *normalis* fo. *brevipes* Kuntze, loc. cit. 2: 508. 1891.
Phyla nodiflora var. *sericea* (Kuntze) Moldenke, Phytologia 1: 98. 1934.
P. yucatana var. *parvifolia* Moldenke, op. cit. 2: 141. 1946.
P. strigulosa var. *parvifolia* (Moldenke) Moldenke, op. cit. 2: 233. 1947.

This variety differs from the typical in being smaller in all its parts and more conspicuously canescent-strigose throughout; stems and branches often slightly

woody, internodes often reduced to 1 cm or less long; mature leaves less than 1.5 cm long and to 1 cm wide, the venation plainly impressed above and prominent beneath, imparting a decided plicate appearance to the leaves, the petioles obsolete or 1–2 mm long.

This variety is found in dry sandy soil from Texas and Mexico, the Bahamas and Greater Antilles, through the Lesser Antilles, to Trinidad, Venezuela, and Panama.

PANAMÁ: Taboga Island, 200–300 m, *Jiménez M. 3095* (US).

4. **Phyla nodiflora** (L.) Greene, Pittonia 4: 46. 1899. var. **nodiflora**.

Verbena nodiflora L., Sp. Pl. 20. 1753.
V. capitata Forsk., Fl. Aegypt.-arab. 10. 1775.
Blairia nodiflora (L.) Gaertn., Fruct. Sem. Pl. 1: 266, *pl. 56*. 1788.
Phyla chinensis Lour., Fl. Cochinch., ed. 1. 66. 1790.
Zapania nodiflora (L.) Lam., Tabl. Encycl. Méth. Bot. 1: 59, *pl. 17, fig. 3*. 1791.
Lippia nodiflora (L.) Michx., Fl. Bor. Amer. 2: 15. 1803.
Verbena repens Bertol., Rar. Ital. Pl. Dec. 2: 27. 1806.
Platonia nudiflora Raf., Med. Repos. 5: 352. 1808.
Verbena sarmentosa Willd., Enum. Hort. Berol. 632. 1809.
Zapania repens (Bertol.) Bertol., Rar. Ital. Pl. Dec. 3: 27. 1810.
Bertolonia crassifolia Raf., Chloris Aetn. 5. 1815.
B. scabra Raf. *ex* McMurtie, Sketch Louisv. 214. 1819.
Lippia sarmentosa (Willd.) Spreng. *in* L., Syst. Veg., ed. 16. 2: 752. 1825.
L. repens Spreng. *in* L., Syst. Veg., ed. 16. 2: 752. 1825.
Verbena repens Petagn. *ex* Spreng. *in* L., loc. cit. 2: 752. 1825.
Zapania crassifolia (Raf.) Raf., Herb. Raf. 66. 1833.
Piarimula chinensis Raf., Fl. Tellur. 2: 102. 1836.
Lippia nodiflora α *vulgaris* Walp., Repert. Bot. Syst. 4: 49. 1845.
L. nodiflora var. *sarmentosa* (Willd.) Schau. *in* A. DC., Prodr. 11: 585. 1847.
L. nodiflora var. *repens* (Bertol.) Schau. *in* A. DC., op. cit. 11: 586. 1847.
L. nodiflora α *normalis* Kuntze, Rev. Gen. Pl. 2: 508. 1891.
L. nodiflora α *normalis* fo. *brevipes* Planch. *ex* Kuntze, loc. cit. 2: 508. 1891.

Perennial creeping *herbs*; stems prostrate, mostly rooting at the nodes, usually 30–90 cm long; branches slender, procumbent or ascending, densely appressed-strigillose to minutely puberulent or glabrate. *Leaves* with the blades thick-textured, fleshy when fresh, spatulate or oblanceolate to obovate, sometimes elliptic or cuneiform, 1–7.2 cm long and 0.6–2.5 cm wide, rounded or obtuse (rarely subacute) apically, narrowed into a long- or short-cuneate base, sharply serrate above the middle with sharply acute or acuminate mostly appressed or subappressed teeth, entire basally, minutely or densely strigillose-puberulent on both surfaces or glabrous, the venation usually indiscernible on both surfaces or at least inconspicuous; petioles 2–8 mm long or obsolete, often so broadly cuneate-margined as to appear as though a part of the blade. *Spikes* at first globose, cylindric and elongate in age, 1–2.5 cm long when mature and 6–9 mm in diameter, densely many-flowered; peduncles solitary in each axil, slender, often much elongate, usually much longer than the subtending leaves, 1–11.5 cm long, densely or sparsely appressed-puberulent or strigose with antrorse canescent trichomes, or glabrous; bractlets closely imbricate, obovate or subrhomboid-cuneate, subequaling the corolla-tube, often broadly membranous-margined apically, mucronate-acuminate or muticous, glabrous or finely ciliate. *Flowers* with the calyx hyaline-membranous, flattened, about equaling the corolla-tube, deeply 2-cleft, slightly

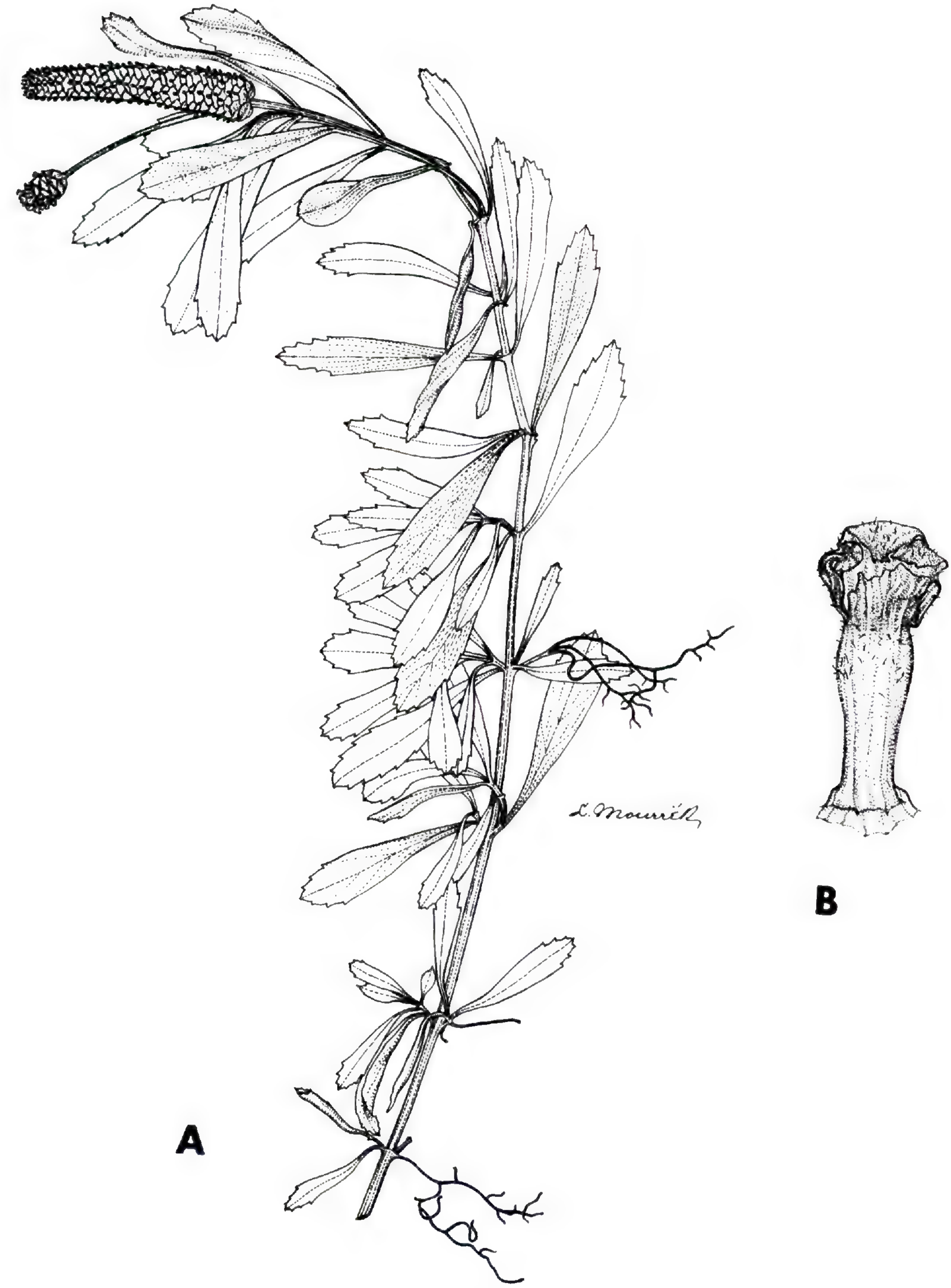

FIGURE 3. *Phyla nodiflora* var. *longifolia* Moldenke—A. Habit (× 1).—B. Flower (× 14). [After *Tyson 2256* (MO).]

2-carinate, the keels puberulent, the lobes lanceolate; corolla purple or pink to white, 2–2.5 mm long, slightly surpassing the bractlets, the limb exiguous, slightly strigillose.

In wet or moist soil, fields, hillsides, clearings, savannas, beaches, and thickets,

widely distributed throughout the subtropical and tropical portions of the Old and New Worlds, especially abundant in moist sandy soil; extremely variable and polymorphic.

Among its many popular names are "cape-weed," "cidron," "fog-fruit," "godet's-weed," "link-weed," "lippia-grass," and "sprain-bush."

CANAL ZONE: Edge of beach, Colón, *Macbride & Featherstone 8* (US). Open field, France Field, *Standley 28589* (US). Common in brushy field, near Fort Randolph, *Standley 28753* (US). Beach, Fort Sherman lighthouse, *Burch et al. 1008* (MO, US). VERAGUAS: Beach, cliffs and adjacent swamp, mouth of Río Concepción, *Lewis et al. 2771* (LL, NY).

4a. **Phyla nodiflora** var. **longifolia** Moldenke, Phytologia 2: 22. 1941.—FIG. 3.

This variety differs from the typical in its much more uniformly elongate leaves, the blades being oblanceolate-cuneate, to 5.5 cm long and 4–10 mm wide, and sharply spreading-dentate toward the apex.

On open sandy flats and salty depressions on or near the seacoast, from the coasts of Louisiana and Texas along the coasts of Mexico and Central America to Colombia and Peru; introduced in Australia and New Guinea.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, Isla Colón, *von Wedel 2945* (MICH, NY). Old Bank Island, *von Wedel 1960* (US). Laguna de Chiriquí and vicinity, *Hart 105* (US). CANAL ZONE: Colón, *Riley 105* (US). Fort Sherman, *Piper 5876* (US). Fort Sherman, near bathing beach, *Tyson 2256* (MO). Open beach, Toro Point, *Duke 4329* (UC). Common in sand along beach, vicinity of Fort Sherman, *Standley 31197* (US). CHIRIQUÍ: Vicinity of San Bartolomé, Peninsula de Burica, *Woodson & Schery 931* (MO, NY). COLÓN: Locality unknown, *Asplund 15156* (S). On sandy beach, Colón, *Moldenke 1230* (LL). Manzanillo Island, *Hayes 713* (NY). On sandy beach, Piña, *Moldenke 1226* (AAU). Along beach and near sea level, vicinity of Viento Frio, *Pittier 4120* (NY). PANAMÁ: Panamá, *Kuntze*, June 1874 (NY, US).

5. **Phyla incisa** Small, Fl. Southeast. U. S., ed. 1. 1012 & 1337. 1903.

Lippia cuneifolia var. *incisa* (Small) Blankinship, Annual Rep. Missouri Bot. Gard. 18: 186. 1907.

L. incisa (Small) E. D. Schulz, Texas Wild Fls. 339. 1928.

Perennial *herbs*; stems mostly prostrate, often swollen and rooting at the nodes, slender, obtusely tetragonal, simple or branched, often purplish, densely or sparsely appressed-strigillose with small white trichomes; branches often numerous, decumbent to ascending or erect, mostly slender, tetragonal, abundantly appressed-strigose with small white trichomes; principal internodes 1.8–5 cm long. *Leaves* often with a cluster of smaller ones in their axils, variable in shape and size, the blades firmly chartaceous, often thick-textured, uniformly green on both surfaces, narrowly oblong or cuneiform to broadly obovate, 1–5 cm long and 2–15 mm wide, acute to obtuse or rounded apically, cuneate basally, sparsely or abundantly dentate above the middle, sparsely or densely appressed-strigillose with small, inconspicuous white trichomes on both surfaces; petioles usually obsolete or only 1–3 mm long. *Inflorescences* 1 or 2 per node, erect, heads at first globose, later cylindric and elongating to 3 cm, 5–7 mm in diameter; peduncles slender, tetragonal, 2–9 cm long, appressed-strigillose; bractlets obovate, 2–3 mm long, acute, abundantly white-strigillose. *Flowers* with the corolla white with a yellow center, the tube 2–2.5 mm long, the limb ca. 2 mm wide. *Fruits* obovoid. $n = 18$.

In open ground, clay or sandy fields, in dried-up depressions, stream- or lake-beds, waste ground, and along roadsides, seashores, and watercourses, from Colorado, Kansas, and Arkansas, west to southern California, east to Georgia, and south through Mexico to Panama; introduced in Iran.

An extremely variable and polymorphic species, apparently hybridizing readily with related species.

CANAL ZONE: Common on flat near river, Fort San Lorenzo, *McDaniels 5173* (MO). COLÓN: Edge of canal, Colón, *Asplund*, 12 June 1920 (S).

4. LIPPIA

Lippia Houst *ex* L., Sp. Pl. 633. 1753; Gen. Pl., ed. 5. 282. 1754.

Dipterocalyx Cham., Linnaea 7: 241. 1832.

Zapania Juss. *ex* Steud., Nom. Bot. Phan., ed. 2. 2: 54. 1841, *pro syn*, nec *Zapania* Lam., Tabl. Encycl. Méth. Bot. 1: 58. 1791, non Scop *ex* A. L. Juss., Ann. Mus. Natl. Hist. Nat. 7: 72. 1806.

Goniostachyum (Schau.) Small, Fl. Southeast. U. S., ed. 1. 1012 & 1337. 1903.

Erect *bushes*, *shrubs*, *undershrubs*, or *subshrubs*, rarely trees, glabrous or variously pubescent with simple trichomes, often hirsute or tomentose, sometimes functionally dioecious, in some grassland regions with herbaceous branches issuing from a basal or subterranean woody xylopodium. *Leaves* decussate-opposite or ternate, rarely alternate or in 4's, simple, deciduous, entire to variously toothed or lobed, exstipulate, petiolate or sessile, flat or rugose above, thin-membranous to heavy-coriaceous, mostly penninerved. *Inflorescences* indeterminate, centripetal, spicate or capitate, solitary or fascicled in the leaf-axils or aggregate in axillary or terminal corymbs or panicles, the spikes mostly contracted into heads or cylindric, not usually conspicuously elongating in fruit, densely-flowered, bractlets conspicuous, not caducous, decussate or many-ranked, often folded, sometimes concave or flat, imbricate, sometimes forming an involucre, mostly large and ovate or lanceolate, often decreasing in size toward the apex of the spike, often accrescent after anthesis. *Flowers* small, sessile, borne singly in the axils of the bracts or bractlets, often more or less 4-ranked, often dimorphic, in some species staminate plants have flowers with well-developed anthers and aborted or non-functional ovary, while carpellate plants have flowers with no stamens or only occasionally 1 or 2 aborted stamens; calyx small, membranous, ovoid-campanulate or compressed and often 2-carinate or -alate, sometimes 2-lipped, the rim 2- or 4-fid or 4-dentate; corolla white or variously colored, hypocrateriform or infundibular, irregular, the tube cylindric, straight or incurved, slender, slightly exserted from the calyx or rarely elongate, equal in diameter throughout or ampliate above, the limb oblique, usually spreading, somewhat 2-lipped, 4-parted, the lobes broad, often retuse apically, the posterior lobe entire, emarginate, or even bifid to about the middle, the lateral lobes exterior, the anterior lobe often larger; stamens 4, didynamous, inserted at about the middle of the corolla-tube; included or slightly exserted, sometimes only 1 or 2 present or completely absent on carpellate plants, the anthers ovate, unappendaged, the thecae parallel, often aborted or absent on pistillate plants; gynoecium often aborted or non-functional on staminate plants, gynoecium syncarpous, the ovary globose, 2-loculed, the ovules

1 per locule, basal and erect or affixed laterally near the base; the style single, often short, the stigma single, incrassate or capitate, oblique or recurved. *Fruits* small, dry, ovoid, included by the fruiting-calyx and sometimes adnate to it, dividing into 2 pyrenes or nutlets at maturity, the pericarp papery and hard, the exocarp membranous and rarely distinct from the pyrenes; seeds without endosperm.

A genus of about 254 species, varieties, and named forms, widely distributed in subtropical and tropical America, a few also in tropical portions of the Old World.

a. Peduncles 1 or 2(–3) per leaf axil.
  b. Flower-heads with large, showy, papyraceous, accrescent bracts to 20 mm long and wide ..... 1. *L. oxyphyllaria*
  bb. Flower-heads with neither showy, accrescent, nor papyraceous bracts; bracts 3–6 mm long.
    c. Leaf-blades more or less scabrous above, the trichomes conspicuously bulbous-based, the bases persistent.
      d. Flower-heads 8–10 mm wide; peduncles usually surpassing the petioles; leaf-blades subcoriaceous, scabrous beneath, short-acuminate to obtuse apically, conspicuously crenate-serrate except basally ..... 2. *L. cardiostegia*
      dd. Flower-heads ca. 5 mm wide; peduncles usually subequaling the petioles; leaf-blades thin-membranous, not scabrous beneath, mostly long-acuminate apically, entire or obscurely serrulate toward the apex.
        e. Branchlets sparsely appressed-strigillose ..... 3. *L. americana*
        ee. Branchlets conspicuously long-pilose ..... 3a. *L. americana* fo. *pilosa*
    cc. Leaf-blades not conspicuously scabrous on either surface, the trichomes not bulbous-based ..... 4. *L. alba*
aa. Peduncles fasciculate or the influorescence paniculate.
  f. Many inflorescences paniculate with 1–3 whorls of pedunculate heads subtended by more or less foliaceous bracts; leaf-blades minutely puberulent beneath ..... 5. *L. costaricensis*
  ff. Inflorescences fasciculate, not paniculate; leaf-blades densely velutinous beneath ..... 6. *L. torresii*

1. **Lippia oxyphyllaria** (Donn. Sm.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1010. 1938.—Fig. 4.

L. substrigosa var. *oxyphyllaria* Donn. Sm., Bot. Gaz. (Crawfordsville) 23: 249. 1897.

Shrubs or small trees, 2–6.5 m high; trunk to 7.5 cm d.b.h.; stems obtusely tetragonal to subterete or terete, glabrous; branches and branchlets obtusely tetragonal to terete, more or less densely appressed-pubescent or pilose, much less so in age. *Leaves* decussate-opposite, petiolate, the leaf-blades thick-textured, oblong-elliptic or elliptic to lance-oblong or lanceolate-elliptic, mostly 1.5–5 cm long and 1–2 cm wide during anthesis, later to 12 cm long and 4 cm wide, mostly acute apically, sometimes somewhat acuminate, acuminate or long-acuminate to cuneate basally and prolonged into the petiole, regularly serrulate or closely crenate from the apex to the base with small rounded teeth, decidedly bullate and rugose above, densely short-pilose and scabrous or asperulous above with many bulbous-based whitish trichomes, densely and softly white-pilose or -tomentose beneath, secondaries and veinlet reticulation prominent; the petioles stout, 5–10 mm long, densely subappressed-pubescent with cinereous trichomes. *Inflorescences* shorter than, equaling, or somewhat surpassing the subtending leaves during anthesis, much shorter than the leaves in fruit, the heads hemispheric,

FIGURE 4. *Lippia oxyphyllaria* (Donn. Sm.) Standl., habit (× 1¼). [After *Stern et al. 1935* (MO).]

1.6–2 cm long and wide during anthesis, hop-like, oblong and to 4 cm long and 3.5 cm wide in fruit; peduncles slender, 1–3 cm long, densely appressed-pubescent, spreading or somewhat recurved; bracts large, ovate or broadly ovate to ovate-lanceolate, papyraceous, reddish, 1–1.8 cm long and 5–8 mm wide during anthesis, later enlarged and to 2 cm long and wide, acute, short-pubescent or puberulent

on the lamina, ciliate-margined, the outers long-acuminate. *Flowers* with the corolla hypocrateriform, white or greenish-white to yellow.

Known only from Costa Rica and Panama, and there called "caragra."

CHIRIQUÍ: Llanos ca. 2 mi. from Bambito woods, in open sunlight, dry habitat, valley of the upper Río Chiriquí Viejo, *White 332* (GH, MO, NY). Vicinity of Boquete, llanos area just S of town, 3500 ft, *Stern et al. 1935* (MICH, MO, US). Between Cerro Vaca and Hato del Loro, 850–1100 m, *Pittier 5387* (NY). Llanos de Volcán, ca. 1300 m, *Allen 1541* (GH, MO, NY). Lava fields near town of Volcán, ca. 4600 ft, *Duke 9182* (BMIC, MO). Llanos region, 1 mi. from El Volcán, *Ebinger 785* (MO). Llanos on slopes of Volcán de Chiriquí and along Río Chiriquí Viejo, 1200 m, *Allen 1008* (GH, MO, NY). COCLÉ: Penonomé and vicinity, 50–1000 ft, *Williams 151* (NY). VERAGUAS: Cañazas, *Tyson 3632* (MO, NY). Trail between Cañazas and foot of Cordillera Central headwaters of Río Cañazas, 300–600 m, *Allen 155* (AAH).

2. **Lippia cardiostegia** Benth., Bot. Voy. Sulphur 153. 1846.

L. brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1009. 1938.

Suffrutescent *bushes*, sometimes *shrubs* or *trees*, 1–5 m high, densely and strictly branched, strong-scented with a pungent marigold odor; stems slender, arching; bark pale-gray or gray, smooth and glabrous; branchlets slender, densely strigose with short whitish trichomes; principal internodes short or elongate; leaves decussate-opposite, the larger leaves petiolate, the blades subcoriaceous, somewhat stiff, dark-green above, paler beneath, broadly elliptic to ovate, sometimes oblong-ovate, 3–6.5 cm long and 1.5–4 cm wide, shortly acuminate to obtuse apically, cuneate-acute or attenuate basally and often contracted-decurrent into the petiole, closely serrate or crenate-serrate along the margins (except basally), roughly scabrous and densely white-punctate with the persistent bulbous bases of the trichomes, often sub-bulate because of the impressed venation, roughly scabrous beneath, the midrib and larger veins prominent, the secondaries ca. 6 per side; petioles slender, 5–14 mm long, strigillose-scabrous. *Inflorescences* axillary, capitate, 2–6 per node, the heads globose, 8–10 mm wide, scarcely elongate in fruit; peduncles slender, 1–2.5 cm long, usually surpassing the petioles, strigillose-scabrellous; bracts small, chartaceous, green or brown, broadly ovate, acute or subacuminate apically, scabrous or glabrate, to 6 mm long in fruit. *Flowers* with the calyx compressed, 2-dentate, scarcely more than 1 mm long, densely white-pilosulous; corolla hypocrateriform, white or greenish-white to pale greenish-yellow or yellow, ca. 3 mm long, the tube slender, glabrous, the limb 1.5 mm wide, the lobes broadly rounded, densely puberulent outside and sparsely puberulent inside.

Rocky and brushy slopes, rocky fields, hedges, thickets, and dry forests, from southern Mexico to Panama.

Known as "chiligua," "coronchoch," "oreganillo," and "orégano montés."

CHIRIQUÍ: Vicinity of the upper Río Chiriquí Viejo, *White & White 103* (MO).

3. **Lippia americana** L., Sp. Pl. 633. 1753.

L. hemisphaerica Jacq., Enum. Syst. Pl. Carib., ed. 1. 25. 1760.
L. pyramidata Crantz, Inst. Rei Herb. 1: 546. 1766.
L. floribunda H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 216. 1817.
L. pauciserrata Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(2): 203. 1863.

Herbs, woody or somewhat woody below, or slender, sprawling, arching, scrambling, or scandent shrubs or undershrubs, 1–5 m high, unarmed, often branching basally, subglabrous, with a strong aromatic odor; trunk sometimes 15–20 cm in circumference; branches elongate, drooping or pendulous to subscandent, light-green, the adult branches subterete, yellowish, glabrous; branchlets tetragonal, sparsely appressed-strigose and glandular-punctate. *Leaves* decussate-opposite or ternate, membranous, widely spreading or reflexed, deciduous, ovate or oblong-lanceolate, shiny, acuminate or long-acuminate apically, acuminate and entire basally and attenuate into the petiole, entire or obscurely crenate-serrate or -serrulate above the middle, scabrous above, pale and glabrous beneath or sparsely strigose on the veinlet-reticulation and pubescent in the vein-axils, the lower leaves ca. 8 cm long and 3.5 cm wide, the upper leaves smaller. *Inflorescence* axillary, capitate; heads hemispheric, ca. 5 mm wide, becoming ovate or pyramidal-subglobose in age, many-flowered, plainly angulate; peduncles 1–3 per leaf-axil, subequaling the petiole; bractlets cuneate-obovate, subequally imbricate and 8-ranked, abruptly cuspidate or broadly obtuse and short-apiculate apically, subequaling the corolla, many-veined, slightly narrower than the calyx villosity, the lower branchlets somewhat larger. *Flowers* not conspicuous; calyx 1–1.5 mm long, equaling or shorter than the corolla-tube, acutely bifid, bifariously villous with long trichomes on the keel, otherwise shortly white-pubescent; corolla small, hypocrateriform, not conspicuous, pale-green or greenish-white to cream, pale-yellow, or white, the tube exiguous, the limb pubescent or hirtellous on the outer surface. *Fruit* obcordate, fuscous or black, smooth, included by the mature calyx.

Woods, thickets, savannas, shrubby hillsides, and deep wooded canyons, Panama to Peru. The type was originally described from Veracruz, Mexico, perhaps in error.

Known popularly as "barelago," "belíta," "mano de Díos," and "oreganito macho."

HERRERA: Vicinity of Ocú, common in brushy places, 100 m, *Allen 4092* (MO). Hill above cantera of Sr. Joaquin Carrizo, in limestone area much cutover and browsed by animals, *Stern et al. 1722* (MICH, MO, US). Banks of Río Santa Maria, *Burch et al.* (MO, US). LOS SANTOS: 3 mi. S of Carreta, ca. 5 mi. S of Las Tablas, *Burch et al. 1248* (MO, US). Punta Mala, *Tyson 2729* (MO).

4. **Lippia alba** (Mill.) N. E. Br. *ex* Britt. & Wils., Sci. Surv. Porto Rico 6: 141. 1925.

Lantana alba Mill., Gard. Dict., ed. 8. 1768.
Verbena globiflora L'Her., Stirp. Nov. 1: 22–23, *pl. 12*. 1786.
Zappania odoratissima Scop., Delic. Fl. Faun. Insub. 1: 34–35, *pl. 15*. 1786.
Zapania lantanoides Lam., Tabl. Encycl. Méth. Bot. 1: 58. 1791.
Z. globiflora (L'Her.) Willd. *in* L., Sp. Pl., ed. 4. 1: 116. 1797.
Lantana lavandulacea Willd. *in* L., Sp. Pl. ed. 4. 3: 319. 1800.
Lippia asperifolia A. Rich. *ex* Marthe, Cat. Pl. Jard. Méd. Paris 67. 1801.
Zapania odorata Pers., Syn. Pl. 2: 140. 1806.
Lippia geminata H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 214. 1817.
Verbena odorata (Pers.) Steud., Nom. Bot. Phan., ed. 1. 873. 1821.
Lantana geminata (H.B.K.) Spreng. *in* L., Syst. Veg., ed. 16. 2: 763. 1825.
L. mollissima Desf., Cat. Hort. Par., ed. 3. 393. 1829.

Lippia citrata Cham., Linnaea 7: 214. 1832.
Lantana lippioides Hook. & Arn., Bot. Beechey's Voy. 305. 1837.
Lippia panamensis Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(2): 201. 1863.
L. havannensis Turcz., loc. cit. 36(2): 202. 1863.
L. crenata Sessé & Moc., Fl. Mex., ed. 2. 140. 1894.

Erect perennial *herbs* or straggly, aromatic, densely puberulent, low, coarse, erect *shrubs* or *subshrubs*, to 2 m tall, with a strong odor of lemon, lime, mint, or sage, sometimes scrambling, procumbent, or semi-procumbent, or more or less decumbent, rarely creeping or scandent, usually much-branched from the base and with long rooting basal suckers; stems many, to 1.5 cm in diameter, rooting at the nodes; branches elongate, slender, ascending or pendulous, sometimes arching, trailing, or prostrate. *Leaves* decussate-opposite or ternate, thickish, aromatic, the blades ovate or oblong, 2–7 cm long and usually 1.2–2.3 cm wide, dark-green above, acute or obtuse apically, conspicuously serrate or serrulate along the margins (except at the very base), mostly cuneate or narrowed into the petiole basally, strigose-hirtellous or puberulent and more or less rugose (when mature) above, densely short-pubescent or soft-velvety to tomentose beneath with cinereous trichomes; petioles slender, 3–8 mm long, cinereous-pubescent. *Inflorescences* axillary, capitate, usually much shorter than the subtending leaves or only subequaling the petioles, solitary or rarely paired in all the upper leaf-axils; heads globose or subglobose to shortly oblong, 8–12 mm long and ca. 8 mm in diameter; peduncles slender; bractlets ovate, 3–5 mm long, acute apically, the lowermost 3–3.5 mm wide, nearly as long as the corolla, not accrescent. *Flowers* fragrant or non-odoriferous; calyx ca. ⅓ as long as the corolla, 2-toothed; corolla hypocrateriform, in various shades of blue, pink, lilac, violet, lavender, mauve, or purple, sometimes white, often yellowish on the inner surface, the tube 4–5 mm long. $2n = 40$ (42?).

Widely distributed through the West Indies, Mexico, Central America, and subtropical and tropical South America to Argentina; introduced and often escaped from cultivation elsewhere.

An extremely variable and polymorphic species; a dozen subspecific entities have been proposed, some of which may be worth maintaining. The extremely hairy southern South American "*globiflora*" form may be distinct.

Over a hundred popular names have been recorded, among the commonest of which are "achueriala," "alfombrilla," "cidreira," "herva cidreira," "orégano," "orégano de burro," "palisado," "salsa limão," "salvia morada," "sauce limón," and "toronjil de España." The plant is widely used medicinally as a sudorific, pectoral, diaphoretic, antispasmodic, emmenagogue, and stomachic. The leaves are used in baths in treating fevers. It is widely cultivated. Cultivated by the Cava Indians (fide *Duke 14436*); used as a tea for diarrhea (fide *Tyson 3611*).

CHIRIQUÍ: Sabana de la Tortuga between El Boquete and Caldera, 300–700 m, *Pittier 3329* (GH). COLÓN: Chagres, *Fendler 220* (MOLDENKE, photo). PANAMÁ: Piria, Río Bayano, ca. 150 m, *Duke 14436* (BMIC, MO). VERAGUAS: Cañazas, *Tyson 3611* (MO).

5. **Lippia costaricensis** Moldenke, Phytologia 1: 424–425. 1940.

Trees, to 18 m high; trunk to 33 cm in diameter; branchlets stoutish or rather slender, acutely tetragonal, often submargined, more or less substrigose-pilose, the

nodes plainly annulate, often conspicuously so, the principal internodes 2–4.5 cm long. *Leaves* decussate-opposite, with a mint-like aroma, chartaceous, uniformly green on both surfaces, narrowly elliptic, 8–18 cm long and 1.5–5 cm wide, rugose, attenuate and acute or acuminate apically and basally, regularly serrulate from the apex to the base with fine rounded and appressed teeth, often subrevolute along the margins, slightly scabrous and minutely strigillose above, glabrescent and merely punctate in age, minutely puberulent beneath, often only on the veins, the stout midrib and 8–10 pairs of slender secondary veins plane above and prominent beneath, the veinlet reticulation abundant, plane but often obscure above, the larger portions subprominulous beneath; petioles slender, 1–2 cm long, usually short, more or less appressed-strigose. *Inflorescences* axillary, mostly paniculate with 1–3 whorls of capitate branches subtended by more or less foliaceous bracts; heads 5–10 mm wide, conspicuously bracteolate; bractlets large, ovate, stramineous, the lowermost ca. 6 mm long and 4 mm wide, minutely puberulent. *Flowers* with the corolla hypocrateriform, yellow.

In forests, clearings, and volcano slopes, Costa Rica and Panama.

"Caragra."

CHIRIQUÍ: Slopes of Volcán Baru near the town of Cerro Punta, 600 ft, *Stern & Chambers* 88 (AAH, MO, MOLDENKE).

6. **Lippia torresii** Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1010. 1938.

Large forest *trees*, 4–24 m high; crown broad, flat or rounded; trunk 15–90 cm in diameter, the bark neutral gray, brownish, or light-brown to gray-brown, neutral-brown, or dark-brown, moderately striate with raised ridges, rough; branches wide-spreading, the young branchlets greenish, acutely angular, roughly square in cross-section, densely hispidulous with short sordid trichomes. *Leaves* decussate-opposite, aromatic with a mint-like odor, the blades thick and fleshy when fresh, membranous when dry, barely or slightly stiffened, bright-green or dark emerald-green above, light-green to gray-green beneath, not shiny, ovate-oblong, mostly 12–21 cm long and 6–9 cm wide, acute or subacuminate apically, sharply crenulate along the margins, rather abruptly cuneate-attenuate basally, scabrous and rugose above, sparsely villosulous but soft to the touch above and more or less bullate with sharply reticulate veinlets, much paler and densely velutinous-pilose beneath with straight and spreading but more or less entwined trichomes throughout, the secondary veins ca. 10 per side, arcuate-ascending at a rather broad angle; petioles slender, 1.5–2.5 cm long, densely hispidulous. *Inflorescences* with the peduncles axillary, fasciculate, slender, ca. 1.5 cm long, puberulent or densely hispidulous; heads small, round or flattened, globose and 1 cm in diameter when in fruit; bractlets light-green, violet-purple apically, glanduliferous, slightly glutinous, membranous and accrescent in fruit and then much blown by the wind, venose, ciliolate on the margins, otherwise glabrous, broadly rounded apically. *Flowers* densely capitate, not fragrant but attracting many insects; calyx almost 2 mm long, densely villosulous; corolla hypocrateriform, various shades of yellow to greenish-white or white, almost completely glabrous on the outer surface, the tube slender, 2 mm long, the 4 or 5 lobes expanded or reflexed, ca. 1 mm long, puberulent above.

In and at the edges of forests, potreros, and pastures, on brushy slopes, and in the fog zone, Costa Rica and Panama.

Known as "caragra," "caragra negra," and "caragre."

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1500–2000 m, *Allen 1481* (GH, MO, NY). Near Cerro Punta, 2000 m, *Allen 1565* (GH, MO, NY). Cerro Punta, forest adjacent to Hacienda Carinthia, 6000 ft, *Stern & Chambers 78* (BAS, MOLDENKE). Finca Collins, vicinity of Boquete, "El Velo," 6150 ft, *Stern et al. 1997* (MICH, MO, US).

5. STACHYTARPHETA

Stachytarpheta Vahl, Enum. 1: 205. 1805, nom. cons.

Serarda Adans., Fam. Pl. 2: 12. 1763.
Sherardia Vaill. *ex* Adans., Fam. Pl. 2: 198. 1763.
Valerianoides Boeth. *ex* Medic., Phil. Bot. 1: 177. 1789, nom. rejic.
Abena Neck., Elem. 1: 296. 1790.
Vermicularia Moench, Meth. Suppl. 150. 1802, nom. rejic.
Cymburus Salisb., Parad. Lond. *pl. 49*. 1806.
Melasanthus Pohl, Pl. Bras. Ic. 1: 75, *pl. 60*. 1827.
Stachytarpha Link, Enum. Hort. Berol. 1: 18. 1827.
Tarpheta Raf., Fl. Tellur. 2: 103. 1836.

Annual or perennial *herbs* or low *shrubs*, glabrous throughout or villous with simple trichomes. *Leaves* opposite or alternate, dentate, often rugose. *Inflorescences* terminal, spicate, the spikes elongate or abbreviated, densely or loosely many-flowered, occasionally few-flowered, the flowers sessile or semi-immersed in furrows in the rachis of the spike, each solitary in the axil of a bract; bracts small and narrow, appressed or spreading, or large and ovate or lanceolate, often rigid and imbricate, persistent. *Flowers* with the calyx long, narrowly tubular, membranous or herbaceous, 5-costate, 5-lobed, or 5-dentate apically, the teeth equal or unequal, unchanged in fruit or sometimes variously split in age; corolla white, blue, purple, or red, gamopetalous, usually hypocrateriform, the tube cylindric, straight or incurved, slender throughout or ampliate apically, the limb spreading, 5-parted, the lobes broad, often orbicular, obtuse or retuse apically, equal or more or less unequal; perfect stamens 2, anterior, inserted above the middle of the corolla-tube, included, the filaments short, the anthers unappendaged, the thecae divergent and dehiscing in one continuous line, staminodes 2, posterior, small or minute; ovary 2-loculed, each locule 1-ovuled, the ovule attached laterally near the base of the locule, the style elongate, filiform, the stigma terminal, orbicular, capitate or subcapitate. *Fruits* oblong-linear, dry, included by the fruiting-calyx, splitting at maturity into 2 long, hard, narrow, truncate, 1-seeded cocci; seeds erect, linear, without endosperm.

A genus of about 140 species and infraspecific entities, widely distributed in subtropical and tropical America, with a few (mostly naturalized) in tropical Asia, Africa, and Oceania.

a. Rachis heavy and thick, deeply excavated (furrowed) in fruit ..... 1. *S. jamaicensis*
aa. Rachis slender, shallowly excavated (furrowed) in fruit.
  b. Spikes glabrous or subglabrous throughout, the bracts 5–7 mm long ..... 2. *S. guatemalensis*
  bb. Spikes more or less puberulent throughout, the bracts about 4 mm long; leaf-blades mostly smaller and rounded or obtuse apically ..... 3. *S. cayennensis*

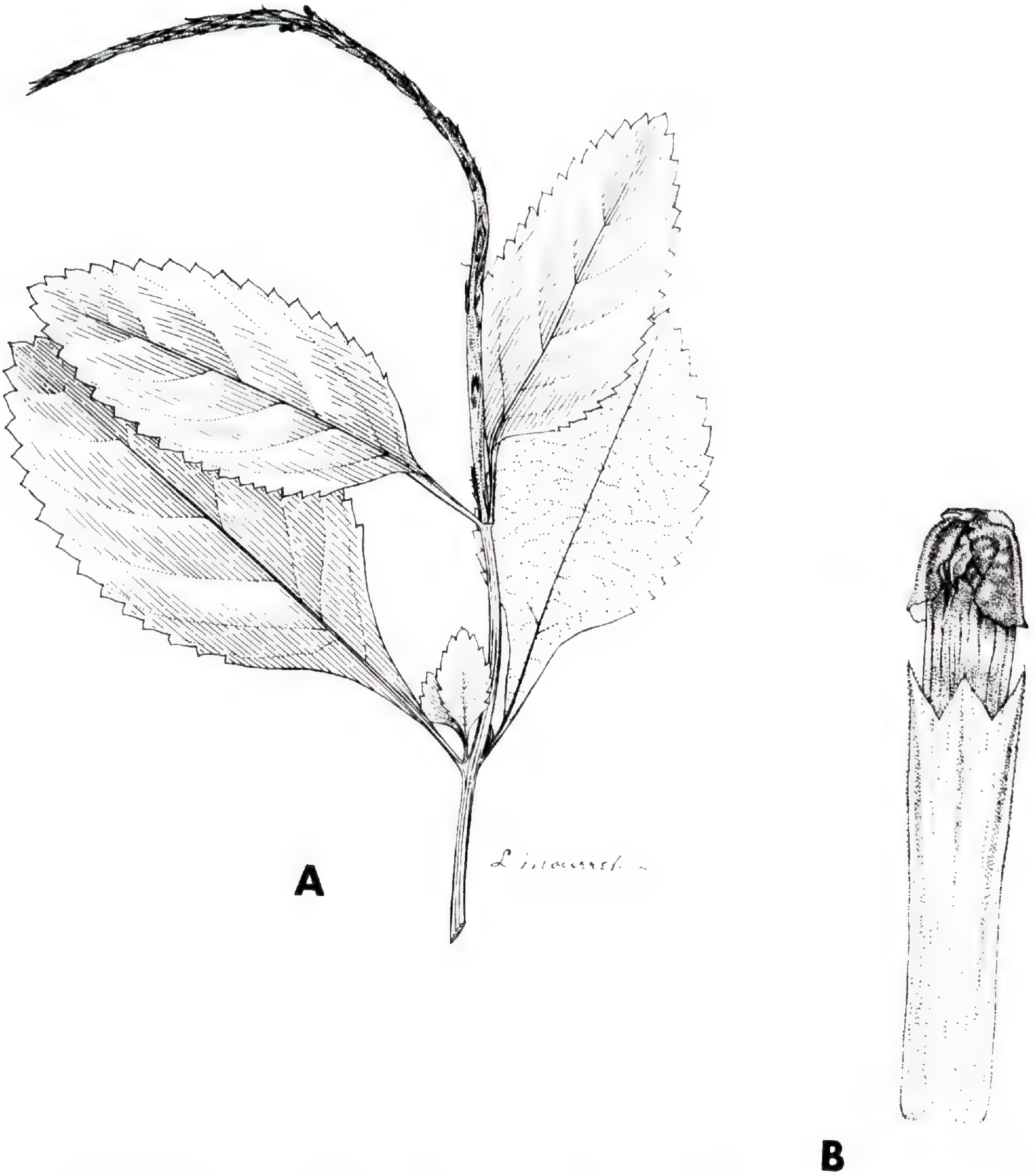

FIGURE 5. *Stachytarpheta jamaicensis* (L.) Vahl—A. Habit (× 5/8).—B. Flower bud (× 8½). [After *Elias 1685* (MO).]

1. **Stachytarpheta jamaicensis** (L.) Vahl, Enum. 1: 206. 1804.—FIG. 5.

Verbena jamaicensis L., Sp. Pl. 19. 1753.
Zapania jamaicensis (L.) Lam., Tabl. Encycl. Méth. Bot. 1: 59. 1791.
Vermicularia decurrens Moench, Suppl. Meth. Pl. 150. 1802.
Stachytarpheta marginata Vahl, Enum. 1: 207. 1804.
S. pilosiuscula H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 226. 1817.
S. mexicana Steud., Nom. Bot. Phan., ed. 1. 873. 1821, nom. nud.
S. bogoriensis Zoll. & Mor. *in* Mor., Syst. Verz. Zoll. 52. 1845–1846.
Valerianodes jamaicense (L.) Kuntze, Rev. Gen. Pl. 2: 509. 1891.
Abena jamaicensis (L.) A. S. Hitchc., Annual Rep. Missouri Bot. Gard. 4: 117. 1893.
Stachytarpheta surinamensis Miq. *ex* Pulle, Enum. Pl. Surinam. 402. 1905.
S. friedrichsthalii Hayek, Feddes Repert. 3: 272. 1907.
S. indica var. *jamaicensis* (L.) Razi, Jour. Mysore Univ. 7(4): 63. 1946.

Herbs, 6–12 dm high, shiny, often purplish throughout, sparingly pubescent or glabrate throughout, sometimes slightly woody basally; stems and branches dichotomous, subtetragonal, usually glabrate except for the lanuginous-pilose nodes. *Leaves* alternate or opposite, rather fleshy when fresh, thin-chartaceous or membranous in drying, oblong to oval or ovate (rarely rounded), 2–8 cm long and 1.2–5 cm wide, obtuse or acute apically, coarsely serrate along the margins with acute and spreading or appressed teeth and more or less ciliate-scabrous, cuneate-narrowed basally and prolonged into the margined petiole, which is as long as the blade or shorter, glabrous on both surfaces or slightly pilosulous on the veins beneath, not usually blackening in drying. *Spikes* terete, stout, stiff, often flexuous, 1.5–5 dm long, glabrous throughout; rachis conspicuously incrassate, the deep furrows much narrower than the rachis itself, especially at maturity. *Flowers* at first erect, later immersed in the thickened rachis; bracts medium-size or comparatively small, lanceolate or oblong-lanceolate, 5–8 mm long and ca. 2 mm wide, aristate-acuminate apically, striate, scabridous, the margins scarious and obscurely ciliolate; calyx compressed, ca. 5 mm long or about as long as the subtending bract, the rim bifid, the teeth triangular or triangular-ovate, completely immersed in the furrows of the rachis in fruit; corolla hypocrateriform, blue or violet to purple, 8–11 mm long, the tube slightly curved, the limb ca. 8 mm wide; style included.

The species is widely distributed throughout tropical and subtropical America from Alabama through the West Indies, Mexico, and Central America to Ecuador and Brazil; introduced in parts of tropical Africa, Madagascar, the islands of the Indian Ocean, tropical Asia, Australasia, and Oceania.

Numerous subspecific taxa have been proposed.

The juice of the leaves, roots, or the entire plant is used in many countries as a tonic, emetic, expectorant, sudorific, cathartic, anthelmintic, emmenagogue, stimulant, antihepatic, purgative, depurative, emolient, and cooling agent. *Stachytarpheta jamaicensis* is used locally in various parts of its range in the treatment of headaches, earaches, malaria, tertian fever, yellow fever, amenorrhea, gonorrhea, diarrhea, syphilis, erysipelas, dropsy, jaundice, contusions and wounds caused by blows, liver troubles, stomach affections, ulcers, intestinal worms, and nervous pains. Among its 100 or more popular names are "berbena," "blue porterweed," "gervão," "Jamaica vervain," "rinchão," "verbena azúl," "verbena cimarrona," "verbena manza," and "verbena morada." Medicinal herb (fide *Kirkbride & Bristan* 1583); "roots and/or leaves used alone or taken with alacran for liver problems either taken as a bath or as a tea" (fide *Duke 10938*).

BOCAS DEL TORO: Bocas del Toro, *Carlton 144* (NY, US). Edge of river and railways and adjacent rainforest, Changuinola to 5 mi. S at junction of Río Changuinola and Río Teribe, 100–200 ft, *Lewis et al. 908* (MO, US). Bar Mouth, Changuinola Valley, *Dunlap 514* (F, US). Rainforest by river, Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 1963* (MO). Isla Colón, vicinity of Chiriquí Lagoon, *von Wedel 2852* (MO, NY). River bank and beach, Santa Catalina, *Blackwell et al. 2707* (LL). Water Valley, *von Wedel 625* (MO). CANAL ZONE: Aspinwall, *Hayes*, June 1861 (BM). Barro Colorado Island, clearing of French Canal, 1 mi. N of laboratory, *Chickering 20* (MICH). Shore at French Lock site, *Woodworth & Vestal 739* (BARRO, F). Gross Point, *Aviles 898* (F). Orchid Island, *Kenoyer 507*, in part (US). Cerro Gordo, near Culebra, 50–290 m, *Pittier 2155* (NY, US). Chagres, *Fendler 219* (F, US). Beach ca. 0.5 mi. inland from mouth of Chagres River, *Burch et al. 1014* (MO). Common, brushy

field, near Fort Randolph, *Standley 28756* (US). Fort Sherman, *Tyson & Blum 1650* (MO); on beach, roadside, *Porter et al. 4983* (LL). In clays of disturbed area, open beach, Toro Point, *Duke 4327* (UC). U. S. Army Tropic Test Center, *Dwyer 7194* (MO). Vicinity of Fort Sherman, common, thicket along beach, *Standley 31140* (US); common, sand along beach, *Standley 31198* (US). Rainforest by road, NW shore of Gatun Lake, ca. 4 mi. S of Río Chagres, *Lewis et al. 1822* (MO). Monkey Hill and vicinity, *Cowell 18* (NY). Near Old Fort San Lorenzo, *Piper 5981* (US). CHIRIQUÍ: Vicinity of Boquete, 1200–1500 m, *Woodson & Schery 768* (MO, NY). Second growth, cultivated areas, and roadsides, from Boquete to 3 mi. N, 3300–4200 ft, *Lewis et al. 571* (MO). Vicinity of San Bartholomé, Peninsula de Burica, *Woodson & Schery 927* (NY). COLÓN: Vicinity of Camp Piña, 25 m, *Allen 3673* (MO, NY, S). Colón, *Lehmann 1009* (BM). María Chiquita, common near bank of beach, thickets near beach, *Dwyer & Kirkbride 7789* (MO). Along shore of beach, *Ebinger 437* (MO). Beach and adjacent roadsides, Nuevo Chagres, *Lewis et al. 1863* (MO). On sandy beach, Piña, *Moldenke 1227* (AAU, LL). *1228* (AAU). Roadside, road to Piña, *Hayden 320* (MO, NY). Waste ground, open grounds, and swampy meadows around Portobelo, 0–20 m, *Pittier 2465* (US). Beach and adjacent area, S of Río Piedras, *Lewis et al. 3165* (LL). DARIÉN: Village of Mannene, *Kirkbride & Bristan 1583* (MO). Vicinity of Vera Cruz, *Duke 6066* (AAU). LOS SANTOS: Beach at Monagre, *Burch et al. 1207* (MO). PANAMÁ: Rocky beach, Chimán, *Lewis et al. 3316* (AAU). San Miguel Island, *Duke 10938* (MO). Taboga Island, *Pittier 3617* (US); on loose trial slopes, *Macbride 2812* (F, MO, US); ca. 0–186 m, *Woodson et al. 1448* (NY). Beach and sandy areas behind, Vera Cruz, *Lewis et al. 3020* (LL). SAN BLAS: Common, airport at Irandi, *Duke 6501* (MO). Suskatupu Island, 0–150 ft, *Elias 1685* (MO).

2. **Stachytarpheta guatemalensis** Moldenke, Publ. Carnegie Inst. Washington 522: 181. 1940.

Herbs or *small shrubs*, to 1.3 m high, abundantly branched; stems and branches slender, mostly acutely tetragonal and margined, glabrous or sparsely pilosulous toward the apex and at the annulate nodes. *Leaves* decussate-opposite; the blades thin-chartaceous or membranous, ovate-elliptic, 3–10 cm long and 1.5–4.5 cm wide, mostly acute apically, abruptly long-cuneate into the petiole basally (the basal petiole-like acumination 1–3.5 cm long), regularly crenate-serrate from below the widest part to the apex, glabrous or subglabrate and shiny on both surfaces; petioles less than 1 cm long or obsolete, but the attenuate leaf-base simulating a petiole. *Spikes* slender, weak and flaccid, 6–17 cm long, erect, densely many-flowered, glabrous or subglabrate throughout; rachis 1–2.5 mm in diameter, the furrows as wide as the rachis, the flowers imbricate, spreading during anthesis, closely appressed before and after anthesis; bractlets narrowly lanceolate, 5–7 mm long, aristate-acuminate apically, scarious-margined toward the base, somewhat divaricate-spreading. *Flowers* with the mature calyx equaling or slightly surpassing the bractlets, mostly coarctate-rostrate apically after anthesis; corolla hypocrateriform, blue to violet or purple.

In forest, thickets, swamps, and waste places, at forest edges, and on savannas, Mexico to Panama.

The plant is known as "camaq olal," "San Diego," "verbena," and "vervena." The boiled juice is sometimes used by natives as a remedy for dysentery.

COCLÉ: Hills NE of El Valle de Antón, disturbed forest edges, 2000 ft, *Lewis et al. 1790* (MO, US). DARIÉN: House number 22, ca. 10 mi. S of El Real on the Río Pirre path from Pucro to Río Pucro, *Duke 5370* (MO). PANAMÁ: Sandy and rocky riverbanks, tributary of Río Chagres, 5 mi. SW of Cerro Brewster, *Lewis et al. 3507* (MOLDENKE). Savannas near Chepo, *Duke 6046* (MO). Roadside between Chepo and Río Bayano, *Porter et al. 5175* (AAU). 3 mi. E of El Llano at Finca Risso, *Tyson 1730* (MO).

3. **Stachytarpheta cayennensis** (L.-C. Rich.). Vahl, Enum. 1: 208. 1804.

Verbena cayennensis L.-C. Rich., Actes Soc. Hist. Nat. Paris 1: 105. 1792.
V. dichotoma Ruiz & Pav., Fl. Peruv. Chil. 1: 23, *pl. 34*. 1798.
Stachytarpheta dichotoma (Ruiz & Pav.) Vahl. Enum. 1: 207. 1804.
S. umbrosa H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 227. 1817.
S. veronicaefolia Cham., Linnaea 7: 246. 1832.
Lippia cylindrica Scheele, Linnaea 17: 351. 1843.
Valerianodes cayennense (L.-C. Rich.) Kuntze, Rev. Gen. Pl. 2: 510. 1891.
Abena cayennensis (L.-C. Rich.) A. S. Hitchc., Annual Rep. Missouri Bot. Gard. 4: 117. 1893.

Herbs or *shrubs*, 1–2.5 m high, much branched; stems and branches subterete, varying from loosely pilose to glabrate. *Leaves* decussate-opposite, the blades membranous, ovate to elliptic, 3–7 cm long and 1.6–2.4 cm wide, obtuse or rounded (rarely subacute) apically, regularly crenate-serrate with subacuminate teeth, narrowed or obtuse basally and more or less cuneate-decurrent into the petiole, scabrate above with sparse strigillose trichomes, not at all rugose, mostly glabrate beneath except for the appressed-strigillose veins, often brunnescent in drying. *Spikes* slender, flaccid, to 34 cm long, mostly glabrous or subglabrate throughout or only slightly pilosulous; rachis scarcely or slightly incrassate, the furrows about as broad as the rachis; bractlets narrowly linear or subulate, setaceous-acuminate or aristate, scarious along the margins. *Flowers* spreading during anthesis; calyx compressed ca. 4 mm long, 4-costate, glabrate, the rim 4-subulate-dentate, about equaling or surpassing the subtending bractlet; erect and half-immersed in the furrows of the rachis in fruit; corolla pale-blue to purple, hypocrateriform, the tube about equaling the calyx, the limb small, ca. 5 mm wide; style included.

On banks and hillsides, in thickets and waste places, on beaches, and along streams and roadsides, widely distributed in tropical America from Mexico and the Greater Antilles, throughout Central America and the West Indies to Peru and Argentina; introduced in Hawaii and in portions of the Old World.

Among its many popular names are "cola de millo," "gervão," "gervão verdadeiro," "verbena," "verbena falsa," and "verbena negra." Employed as a sudorific, diuretic, febrifuge, tonic, and stimulant, and used in the treatment of ulcers and yellow fever.

CANAL ZONE: In pasture ca. 2 mi. N of Gamboa and Boat Club, *Lazor 3499* (MO). Hills between Río Grande and Pedro Vidal, on road to Arraijan, 50–150 m, *Pittier 2705* (NY, US). Around Tabernilla, along the railway, 20–25 m, *Pittier 2816* (NY, US). Hillside, west side of Canal, Balboa, *Rowlee & Stork 985* (NY, US). In thickets, western slope of Ancon Hill, *Woodson et al. 719* (MO, NY). COCLÉ: Disturbed forest edges, hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1790* (BMIC). PANAMÁ: Camino de La Granja, *Bro. Heriberto 167* (NY, US). La Exposición, *Bro. Heriberto 241* (US). Low thicket, Las Sabanas, *Standley 24870* (US). Moist thicket, scarce, between Las Sabanas and Matías Hernández, *Standley 31896* (US). Panamá, *Hayes 723* (NY). Moist thicket, Taboga Island, *Standley 27013* (US). Commonly in grassy field, Tumba Muerto Road, near Panamá, *Standley 29767* (US).

6. PRIVA

Priva Adans., Fam. Pl. 2: 505. 1763.

Burseria Loefl., Iter Hisp. 194. 1758.
Zapania Lam., Tabl. Encycl. Méth. Bot. 1: 58. 1791.
Streptium Roxb., Pl. Corom. 2: 25, *pl. 146*. 1798.
Tortula Roxb. *ex* Willd., Sp. Pl., ed. 4. 3: 359. 1801.

Herbaceous, caulescent perennials, mostly harshly pubescent throughout; stems, branches, and branchlets more or less tetragonal, often decumbent. *Leaves* decussate-opposite or subopposite, simple, exstipulate, thin-membranous, sessile or petiolate. *Inflorescences* terminal and axillary, indeterminate, racemiform, often subspicate during anthesis, narrow, erect or subflexuous. *Flowers* mostly small, solitary in the axil of a small bractlet, arranged in a spirally alternate or pseudosecund manner on an elongated rachis, never whorled; calyx gamosepalous, tubular during anthesis, 5-ribbed, slightly 5-plicate, slightly irregular or nearly regular, terminating in 4 short and equal or subequal teeth, persistent, accrescent, enlarging with and investing the fruit; corolla gamopetalous, more or less irregular, hypocrateriform or infundibular, surpassing the calyx, the tube straight or somewhat curved, more or less ampliate apically, the limb spreading, oblique, more or less bilabiate, the abaxial lip 3-lobed with 1 large central and 2 medium-sized lateral lobes, the axial lip 2-lobed, with usually very small lobes; fertile stamens 4, didynamous, the upper pair better developed and usually inserted slightly above the middle of the corolla-tube, the lower pair inserted approximately at the middle of the tube, all included or equaling the tube, the anthers erect, ovate or oblong, 2-thecate, dorsifixed at or below the middle, introrse, the connective usually conspicuously thickened and sagittate, unappendaged, the thecae parallel or divergent basally, dehiscing by longitudinal slits, the fifth (posterior) stamen reduced to a minute staminode or absent; ovary 4-loculed or (by abortion) 2-loculed, the ovules basal, erect, anatropous, 1 per locule, the style usually equaling the lower stamens, 2-lobed apically, the anterior lobe longer and recurved or erect, stigmatiferous apically, the posterior lobe reduced, minute and tooth-like not stigmatiferous. *Fruit* a dry, often woody schizocarp included by the fruiting-calyx, composed of 2 usually similar, 2(or by abortion 1)-loculed cocci which separate easily at maturity, the pericarp hard, the dorsal surface echinate, scrobiculate or ridged, the commissural surface excavated, concave, or plane; seeds lacking endosperm.

A genus of 26 species and infraspecific entities, widely distributed in subtropical and tropical Asia, Asia Minor, Africa, and America.

a. Corolla blue or lavender to violet, purple, or pink ..... 1. *P. lappulacea* fo. *lappulacea*
aa. Corolla white ..... 1a. *P. lappulacea* fo. *albiflora*

1. **Priva lappulacea** (L.) Pers. Syn. Pl. 2: 139. 1806. fo. **lappulacea**.—FIG. 6.

Verbena lappulacea L., Sp. Pl. 19. 1753.
Zapania lappulacea (L.) Lam., Tabl. Encycl. Méth. Bot. 1: 59. 1791.
Priva echinata A. L. Juss., Ann. Mus. Natl. Hist. Nat. 7: 69. 1806.
Tamonea lappulacea (L.) Poir. *in* Lam., Encycl. Méth. Bot. 7: 568. 1806.
Priva lamiifolia Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11(2): 325. 1844.

Perennial herbs to 1 (or 2?) m high; stems spreading and often decumbent or procumbent; branches prostrate to ascending or even erect, often sulcate, pilose-pubescent with curved or uncinate trichomes, glabrescent in age below, the larger nodes usually annulate with a band of longer trichomes. *Leaves* membranous, ovate, 1.4–14.5 cm long and 9–85 mm wide, acute or acuminate apically, uniformly and coarsely serrate (except basally and on the acumination) with blunt or acute and appressed teeth, mostly subtruncate or subcordate (or acute when young)

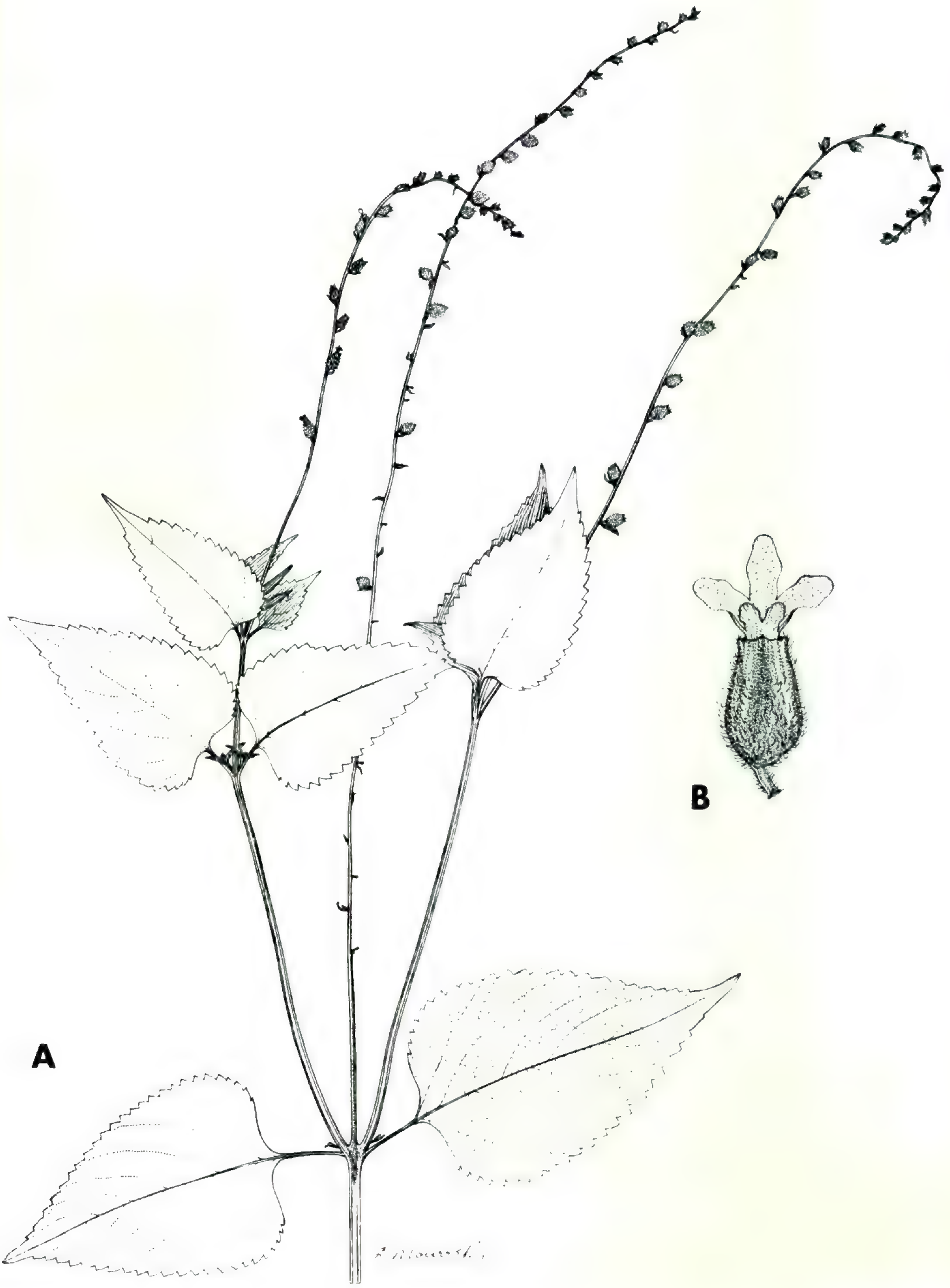

FIGURE 6. *Priva lappulacea* (L.) Pers.—A. Habit (× ⅝).—B. Flower (× 6¼). [After *White & White 194* (MO).]

basally, with the center short-cuneate, pilose or strigose above with scattered whitish bulbous-based trichomes, scattered, pilose and puberulent beneath, the veinlet reticulation inconspicuous; petioles slender, 8–30 mm long, more or less pilose with scattered whitish trichomes. *Inflorescences* terminal on stems and branches, 4.5–21 cm long and 5–15 mm wide, many-flowered, the flowers loosely alternate on the puberulent-pilose rachis; peduncles slender 8–58 mm long, more or less puberulent-pilose, the uppermost leaves at the base of the peduncles often much reduced; bractlets usually surpassing the pedicels during anthesis. *Flowers* with the calyx oblong-campanulate, 2–3.1 mm long and ca. 2.3 mm wide, densely short-tomentose with uncinate trichomes ca. 0.3 mm long and interspersed among them scattered straight trichomes ca. 0.5 mm long, obscurely 5-ribbed only toward the apex, the rim 5-apiculate with minute apiculations, in fruit broadly ovate, thin-membranous, conspicuously inflated, enclosing the fruit and shortly beaked apically, 5–7 mm long and 3–4.5 mm wide, densely hispidulous with uncinate whitish trichomes; corolla hypocrateriform, usually blue to lavender, violet, purple, or pink, with a few scattered trichomes on both surfaces, the tube broadly cylindric, straight, ca. 3.6 mm long on the axial and 3.3 mm long on the abaxial side, ca. 1.8 mm wide, the central abaxial lobe ca. 1.8 mm long and 1.5 mm wide, the 2 lateral abaxial lobes each ca. 1.2 mm long and 0.7 mm wide, the 2 small axial lobes each ca. 1 mm long and wide, all broadly elliptic-lingulate and rounded; upper pair of fertile stamens inserted ca. 1.5 mm and the lower pair ca. 1 mm above the base of the corolla-tube, included; ovary 4-loculed and ovulate. *Schizocarps* oblong, conspicuously quadrangular, composed of 2 identical, joined, 2-loculed, woody cocci, glabrous, each mature coccus ca. 3 mm long and 2 mm wide, the dorsal surface echinate with 2 parallel longitudinal marginal rows of short straight sharp spines 0.5–1 mm long, the area between the rows of spines obscurely scrobiculate-reticulate or transversely ridged, the sides transversely ridged with slender subparallel ridges, the commissural surface plane or nearly so, not margined.

Widespread in open and waste places, along roadsides, in fields and pastures, thickets and hammocks, on brushy slopes and rocky banks, and along fences and hedgerows, in the subtropics and tropics of America from Florida through the West Indies, and from Texas and Mexico through Central America to Peru, Brazil, and Bolivia; also naturalized in Java.

Among its many popular names are "amor seco," "berbenilla," "cadillito," "cadillo," "mozote," "mozote de gallina," "pegapega," "stick-tight," and "velvet-bur."

BOCAS DEL TORO: Bocas del Toro, *Carlton 147* (GH, US). Region of Almirante, *Cooper 129* (F, P). Changuinola Valley, *Dunlap 193* (US). Without locality, *von Wedel 413* (MO). Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 1495, 1601* both (MO). CANAL ZONE: Sosa Hill, on brushy slope, *P.C. Standley 26473* (US). Near Fort Kobbe, *Duke 3964* (MO). In sun, roadbank near Survival School, Curundu, *Tyson 1070* (MO). Weed in sun, Gatún railroad station, *Tyson 3525* (MO). Lawn weed, Fort Sherman at point, *Tyson & Blum 3776* (MO). Just beyond salt spray, on main post near beach, *Tyson 2239* (MO). S end of island in Miraflores Lake, open sunlight, moist habitat, *White 243* (MO), *P. White 254* (MO, NY), *White & White 194* (MO). CHIRIQUÍ: Vicinity of Puerto Armuelles, 0–75 m, *Woodson & Schery 835* (MO, NY). COLÓN: Without locality, *Cooper 259* (NY). DARIÉN: Vicinity of Yapé, ca. 30 m, *Allen 853* (F). Loma coast, behind Manene, *Duke 13631a* (BMIC). Path

from Pucro to Río Pucro, *Duke 5368* (MO, MO). Village of Mannene, *Kirkbride & Bristan 1602* (MO). Woods 2 mi. E of Santa Fé, *Tyson et al., Duke 4825* (MO). PANAMÁ: Marragantí, *Williams 1032* (NY, US). Sandy loam soil, cultivated land, Panamá, *Barclay 2496* (BM). Panamá, *Duchassaing s.n.* (P). Open grazed area near Jenine, along Panamerican Highway, Río Cañita, *Duke 3835* (MO). Weeds of Río Pacora just below confluence with Río Corso, *Duke 12045* (MO). Waste places, Taboga Island, *Killip 3178* (US). Area around dirt road to Ojos de Agua where it branches off the Carretera Transisthmica (between Panamá and Colón), ca. 5 mi. N of Panamá, weed on hillside, *Mowbray et al. 5044* (MO). Taboga Island, 0–250 m, *Pittier 3560* (GH, US). Common in moist thicket, Taboga Island, *Standley 27031* (US). Taboga Island, common on brushy slope, *Standley 27917* (CP, US). Taboga Island, near village, *Tyson 5594* (MO). Taboga Island, *Woodson et al. 1454* (F, MO, NY).

Leaves used by the Choco Indians for treating colds and whooping cough ("ros"), (fide *Duke 13631a*).

1a. **Priva lappulacea** fo. **albiflora** Moldenke, Phytologia 17: 114. 1968.

This form differs from the typical form of the species in having pure white corollas. It occurs sporadically throughout the range of the species.

BOCAS DEL TORO: Edge of river and railway and adjacent rainforest, Changuinola to 5 mi. S at junction of Río Changuinola and Río Terebé, 100–200 ft, *Lewis et al. 926* (MO, US). Colón Island, vicinity of Chiriquí Lagoon, *von Wedel 2834* (MICH, MO, NY). CANAL ZONE: Moist thicket, Balboa, *Standley 27157* (CP, US). DARIÉN: Río Balsa between Quebrada Chusomocatre and Río Areti, *Duke 8723* (AAU, MO). PANAMÁ: Sea level, Bella Vista, *Killip 12003* (US). Moist thicket, near Matías Hernández, *Standley 28916* (US).

7. PETREA

Petrea L., Sp. Pl. 626. 1753; Gen. Pl., ed. 5. 275. 1754.

Shrubs, *trees*, or *woody vines*. *Leaves* decussate-opposite or whorled, deciduous, exstipulate, pinnately net-veined, often roughened and with prominent venation. *Inflorescences* axillary or terminal, indeterminate (centripetal), racemose, mostly elongate, many-flowered, often very handsome; bracts mostly small or absent, the bractlets and prophylls small, numerous, caducous. *Flowers* perfect, alternate on the rachis, often distant, each subtended by 1 or more prophylls, the receptacle swollen; calyx mostly regular, the tube cylindric or campanulate, mostly ribbed, membranous during anthesis, normally 5-lobed, the lobes mostly equal, blue or violet to purple or white, mostly longer than the tube, alternate with the corolla-lobes, bearing ventrally at the base of the lobes a thin-membranous, calicinal crest either in the form of a narrow sinuate or 5-toothed coronet or, if 5-cleft to the base, the divisions alternate with the calyx-lobes, erect during anthesis; corolla hypocrateriform, mostly darker blue or darker purple than the calyx or white, mostly slightly irregular, the tube cylindric, urceolate, or infundibular, the basal portion mostly narrow, the upper portion mostly abruptly and widely ampliate, the limb rotate, 5-lobed, the lobes mostly of 2 sizes, the anterior largest or rarely of 3 sizes with the 2 posterior smallest, mostly much shorter than the calyx-lobes and alternate with them, the posterior outside in prefloration; stamens 4, didynamous, inserted close together near the middle of the corolla-tube, included by the tube, the filaments short and slender, the anthers oblong or ovate, dorsifixed near the base, 2-thecate, each theca dehiscing by a longitudinal slit, introrse, the connective mostly enlarged, often surpassing the thecae; staminode present or absent; gynoecium compound but 1-carpelled through the abortion

of 1 carpel, included in the corolla-tube; ovary subglobose or oblong, borne on a more or less conspicuous disk, more or less completely 2-loculed, the ovules 1 per locule, lateral, ascending, hemi-anatropous or imperfectly anatropous, or pendent and orthotropous; the style terminal, the stigma capitate, mostly oblique, more or less distinctly bilobed. *Fruits* drupaceous, completely enclosed by the mature calyx, the exocarp leathery or fleshy, the endocarp hard, more or less completely 2-loculed, forming 2 pyrenes, not easily separating, each pyrene 1-seeded, or by abortion the fruit with 1, 1-seeded pyrene; seeds laterally or apically attached, lacking endosperm; fruiting-calyx incrassate, the tube not much accrescent, mostly losing its blue color but becoming hard and tough and mostly plicate-ribbed, the lobes greatly accrescent, stiffened, reticulate-veined, papery, divergent, acting as wings for floating the fruit, the calicinal crest callose, mostly curving inwards and converging, completely closing the mouth of the calyx-tube.

A handsome genus of 41 species and infraspecific entities, widespread in tropical America from Cuba through the West Indies and from northern Mexico through Central America to southern Brazil, some taxa are naturalized in parts of Indonesia. Several species are widely cultivated for ornament. Fossils are known from the Eocene and Miocene of Europe and California.

a. Leaf-blades becoming deeply bullate above when mature, the venation deeply impressed above and sharply prominent beneath.
  b. Calyx and corolla violet or blue ..... 1. *P. rugosa* var. *rugosa*
  bb. Calyx and corolla white ..... 1a. *P. rugosa* var. *casta*
aa. Leaf-blades not conspicuously bullate above when mature, venation not sharply or conspicuously prominent beneath.
  c. Calyx-tube glabrescent or nearly so.
    d. Calyx and corolla blue or lavender to violet or purple ..... 2. *P. aspera* f. *aspera*
    dd. Calyx and corolla white ..... 2a. *P. aspera* f. *albiflora*
  cc. Calyx-tube densely spreading-hirsute or tomentose.
    e. Leaf-blades glabrous or subglabrous beneath ..... 3. *P. volubilis* var. *volubilis*
    ee. Leaf-blades more or less densely pubescent beneath .... 3a. *P. volubilis* var. *pubescens*

1. **Petrea rugosa** H.B.K. var. **rugosa**, Nov. Gen. Sp. Pl., ed. folio. 2: 229. 1817.

P. obtusifolia Benth., Pl. Hartw. 246. 1846.

Shrubs, to 3 m tall; branches slender, gray, obtusely tetragonal, densely pubescent on the youngest parts, puberulent on older parts, prominently lenticellate. *Leaves* opposite, elliptic or broadly elliptic to oblong, ovate or obovate, 2.5–10 cm long, 2–7 cm wide, apically obtuse or rounded to emarginate, rarely acute, basally rounded or obtuse to truncate, rarely subacute, the margins entire and often somewhat revolute, firmly chartaceous or subcoriaceous when mature, rough to touch on both sides, dark- or gray-green above, much lighter beneath, more or less short-pubescent or merely puberulent and asperulous above, often decidedly bullate when mature, densely pubescent beneath, the venation mostly more or less impressed above and sharply prominent beneath, the larger veins mostly arcuately joined in many loops near the margins; petioles 1–5 mm long, densely puberulent or pubescent. *Inflorescences* appearing after the leaves, abundant, axillary, often clustered toward the tips of the branches, the racemes nutant or erect, 16–50 cm long, 4–5 cm wide, densely many-flowered; pedicels densely puberulent; torus swollen, not ribbed. *Flowers* with the calyx campanulate, blue or violet, firm, ca.

5.5 mm long, ca. 2 mm wide basally and 4 mm wide apically, obscurely 5-ribbed, densely puberulent, the lobes obovate, sinuate-margined, 12–13 mm long, basally ca. 3 mm wide and 5.5–6 mm wide at the widest point, the calicinal crest 5-cleft to the base with membranous, triangular-ovate teeth ca. 1.5 mm long, basally 2 mm wide, apically acute, puberulent dorsally; corolla blue or violet, hypocrateriform, slightly oblique, the tube infundibular, 9–10 mm long, the basal portion narrow-cylindric and ca. 2 mm wide, ampliate to 5 or 6 mm apically, the lower half glabrous and the upper half densely short-pubescent outside, densely puberulent among the stamens within, scattered pilose above and below them, the limb rotate, 5-parted, the anterior lobe largest, broadly elliptic or suborbicular, ca. 6 mm long and 7 mm wide, the remaining lobes ca. 5 mm long and 6 mm wide, all puberulent on both surfaces; stamens inserted ca. 6 and 6.5 mm above the base of the corolla-tube, filaments slightly flattened, ca. 1.5 mm long, scattered long-pilose, anthers oblong, the connective thickened above and mucronate but not surpassing the anthers, scattered short-pilose, staminode absent; ovary subrotund, glabrous; disk conspicuous, slightly wrinkled, glabrous. *Fruiting-calyx* hard and tough, the tube to 6 mm long and 5.5 mm wide, 5-ridged, the lobes firm and stiff, to 14 mm long and 6 mm wide, the calicinal crest hard and firm, converging inwards.

On brushy river bluffs and rocky slopes, generally in dry ground, Colombia and Venezuela to Ecuador, also cultivated.

"Chaparrillo" and "Mamoncillo."

CANAL ZONE: Experimental Gardens, *Higgins 451* (NY).

1a. **Petrea rugosa** var. **casta** Moldenke, Feddes Repert. 43: 48. 1938.

This variety differs from the typical variety in its pure white calyx and corolla. It is known only from the following collection, but probably occurs sporadically throughout the range of the species.

CANAL ZONE: Cultivated, Canal Zone Experimental Gardens, Summit, *Lindsay 452* (NY).

2. **Petrea aspera** Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 211. 1863.—FIG. 7.

Woody *vine*; stems stout, twisting, with small pith, obtusely tetragonal, often deeply sulcate between the rounded angles, gray, glabrate; branchlets slender, sparsely or abundantly lenticellate, otherwise similar to the stems. *Leaves* opposite, mostly large, elliptic, 5.5–25 cm long, 3–11 cm wide, apically varying from obtuse or rounded to short-acuminate, entire, often slightly sinuate-undate along the margins in drying, basally acute, thin-membranous or sometimes heavier and firm or even subcoriaceous when old, uniformly green and mostly smooth to touch, sometimes obscurely scabridous on both surfaces, glabrate or very obscurely and minutely asperulous on both surfaces; vein and veinlet reticulation abundant, the larger veins often subprominulous above, more uniformly subprominulous beneath; petioles stout, 5–9 mm long, glabrate or obscurely pulverulent apically. *Inflorescence* appearing with or after the leaves, axillary, borne at or near the ends of the branches, numerous, erect or nutant, 14–39 cm long, to 8 cm wide in

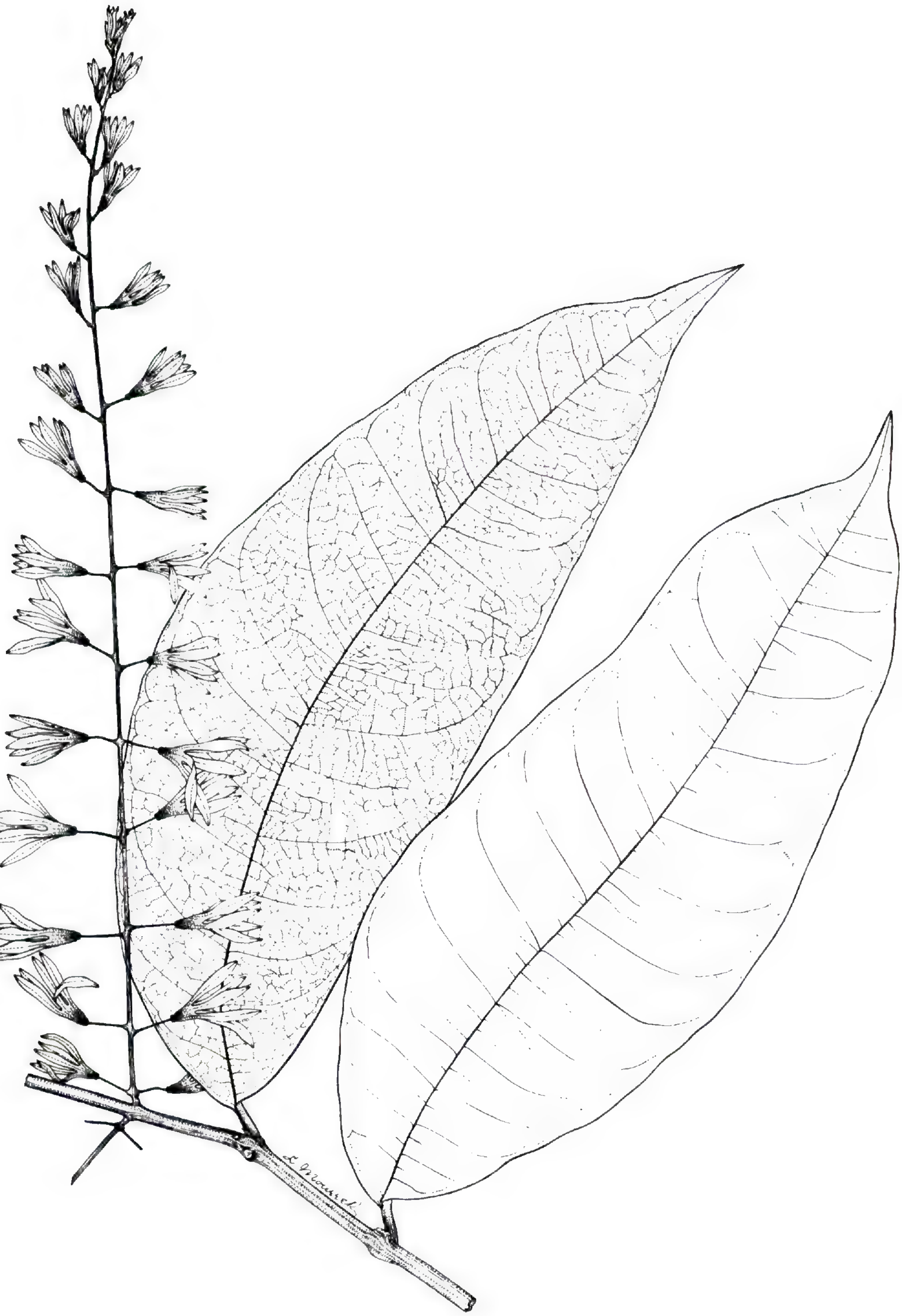

FIGURE 7. *Petrea aspera* Turcz., habit with inflorescence (× ⅝). [After *Allen 960* (MO).]

fruit, racemiform, peduncles 0.5–3.5 cm long; flowering pedicels to 3 cm long; torus swollen, 10-ribbed. *Flowers* with the calyx light-textured, blue or lavender to purple or violet, the tube membranous, subcampanulate, 4.5–5.5 mm long, apically slightly ampliate and 3–5 mm wide, obscurely 5–10-ribbed, not verruculose, glabrate, the lobes thin-membranous, narrowly obovate, 8–21.5 mm long, basally 2.4–3.5 mm wide, 5.5–6 mm wide at the widest point, subacute apically, glabrous on both sides; the calicinal crest 5-cleft to the base, the lobes membranous, triangular-ovate, erect, ca. 2.5 mm long and 1.5 mm wide, apically acute, irregularly and obscurely fringed; corolla hypocrateriform, blue or lavender to purple or violet, the tube infundibular, 16–17 mm long, the basal portion narrow-cylindric and 2–2.5 mm wide, conspicuously ampliate to 7.5–9 mm apically, glabrate outside, within densely short-pubescent from the apex to just below the stamens, the pubescence densest among the stamens, the limb rotate, the anterior lobe largest, broadly obovate, 11–12 mm long, ca. 11 mm wide, rounded, irregularly sinuate, punctate throughout but not pubescent on either surface, the remaining lobes similar but smaller, 9–10 mm long, 10–11 mm wide; stamens inserted ca. 7 and 9 mm above the base of the corolla-tube, the filaments ca. 2 mm long, glabrous or scattered long-pilose, the anthers with slightly thickened connective, not humped nor apiculate, not surpassing the thecae, densely short-pilose; ovary oblong, glabrous; disk glabrous, not ribbed. *Fruiting-calyx* hard and tough, the tube to 6 mm long and 5 mm wide, the lobes stiff, to 22 mm long and 7 mm wide, the calicinal crest callose, converging inwards.

In rainforests and jungles, on the shores of lakes, at the edges of creeks, and along forest trails, ranging from Panama to Brazil and sometimes cultivated in other regions.

"Bejuco de hajo," "biura," "flor de la cruz," "flor de niño," "flor de mayo," "Santa Lucia."

CANAL ZONE: Caladonia Harbor, Mt. Vernon, *Elmore L.41* (MICH). Lion Hill Station, Panama Railroad, *Hayes 1861* (BM, K). Madden Forest Preserve, along Las Cruces Trail and highway, *Lewis et al. 5317* (AAU). Pipeline Road between mile markers 0 and 11.1, ca. 16 mi. N of Gamboa, *Lewis et al. 5427* (MOLDENKE). Experimental Gardens, *Lindsay 259* (NY). Edges of creeks and along forest trails, Gamboa District, *Maggs s.n.* (Cap Pilar Exped. II.48) (F, NY). Railroad relocation between Gorgona and Gatún, 10–50 m, *Pittier 2275* (NY, US). Fort Clayton near old hospital, *Tyson & Blum 3892* (MO). At mouth of Lara River, *Tyson & Loftin 3849* (MO). Paraiso, *Wagner 586* (M). Without locality *Allen 960* (MO, NY, S), *Goldman 1868* (US), *Standley 27609* (US). Albrook Forest, *Blum 2232* (MO), *Epplesheimer s.n.* 1910 (F). Barro Colorado Island, *Bailey & Bailey 636, 648* (both BH), *Bangham 601* (AAH, F), *Croat 4858* (NY), *Frost 196* (F), *Moldenke & Moldenke 19800* (DAO, LEMPERG, NY, SMU, SV), *Shattuck 412* (F, in part), *Wetmore & Abbe 162* (F, GH), *Woodworth & Vestal 385* (F). COLÓN: Along Río Fató, *Pittier 3895* (US). DARIÉN: Near Pinogana, 20 m, *Allen 4293* (MO). Cerro Pidiaque, *Duke 8079* (BMIC, MO). Río Sambu, between Sambu and Río Venado, *Duke 9303* (US). Teotuma, 100 m, *Duke 10071* (MO). Around Pinogana, *Pittier 6531* (US). PANAMÁ: Along Río Chagres between Gamboa and Alhajuela, 30–60 m, *Allen 960* (NY). Panamá, *S. Hayes s.n.* (E). Forests along Río Boqueron above Peluca Hydrographic Station, 90 m, *Hunter & Allen 658* (MO, NY, S). Sabanas, *Bro. Paul 281* (US), *Pittier 6531* (BM, GH, US). Panamá, *Seemann 594* (BM, K), *Williams 702* (NY, US). SAN BLAS: Mainland opposite Ailigandi, *Lewis et al. 195* (MO, US). VERAGUAS: San Francisco, *Powell s.n.* (US). Veraguas, *Seemann 1129* (BM, K). Cañazas, *Tyson 3747* (MO).

2a. **Petrea aspera** fo. **albiflora** Moldenke, Phytologia 18: 421. 1969.

This form differs from the typical form of the species in its white calyx and corolla.

Known only from the collection cited below, but probably occurring sporadically throughout the range of the species. "Bejuco de hajo."

SAN BLAS: Permé, San Blas District, *Cooper 234* (NY).

3. **Petrea volubilis** L., Sp. Pl. 626. 1753.

Petraea volubilis Gaertn., Fruct. & Sem. Pl. 2: 471, *t. 177, fig.* 5. 1791.
P. (volubilis?) mexicana Cham., Linnaea 7: 367. 1832.
Petrea stapelsiae Paxt., Paxton's Mag. Bot. 4: 199. 1838.
Petraea ovata Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 328. 1844.
Petrea sub-serrata Bárcena, Notic. Ci. Estad. Hidalg. 31. 1877, non Cham., 1832.

Woody *vine* or *subshrub* to 13 m tall; branches slender, grayish or brownish, prominently lenticellate, densely puberulent with mostly subappressed brownish hairs (on older wood) or on young shoots hirsute with spreading hairs, obtusely tetragonal or subterete; leaf-scars large and prominent. *Leaves* opposite, elliptic, 3–21 cm long, 1.4–10.6 cm wide, apically acute or short-acuminate, rarely obtuse or emarginate, basally acute or obtusely narrowed, rarely rounded or subcordate, the margins entire, rarely sparsely dentate, often more or less undulate or subrevolute, and densely asperulous on both surfaces, sometimes obscurely short-pubescent along the midrib above and the larger venation beneath, or puberulent, but not densely nor conspicuously so, mostly glabrous or subglabrous; mature petioles stout, 4–13 mm long, densely or sparsely short-pubescent with spreading brownish hairs or puberulent, the axils often with dense fasciculations (actually aborted racemes) of bractlets, densely hirsute, the pubescence ferruginous, firmly chartaceous when mature, scabrous. *Racemes* abundant, solitary, axillary, often clustered near the tips of the branches and branchlets, erect to nutant or pendent, 8–29 cm long, 4–8 cm wide, mostly short and loosely many-flowered; pedicels ca. 8 mm long, obscurely puberulent; torus expanded, not ribbed. *Flowers* with the calyx light, bright blue, the tube cylindric, gradually ampliate apically, ca. 3 mm long, ca. 2 mm wide basally and 2.5–3 mm wide apically, not ribbed, densely pubescent, the lobes oblong, rounded, 13–18 mm long, 4–6 mm wide, membranous and glabrous on both surfaces; the calycinal crest composed of 5 membranous, triangular-ovate erect, acute lobes ca. 1 mm long and wide, sparsely ciliate on the margins; corolla hypocrateriform, bright blue, the tube infundibular, 6–8 mm long, the basal portion narrow-cylindric and 1.5–2 mm wide, conspicuously ampliate to 4 or 5 mm apically, the lower ¾ portion glabrous, the upper ¼ densely puberulent outside, within puberulent and densely villous-pubescent among the stamens, the anterior lobe broadly elliptic, 5–6.5 mm long, 4–4.5 mm wide, slightly sinuate along the margins, densely puberulent on both surfaces, the remaining lobes similar but smaller, 4–6 mm long, ca. 4 mm wide; stamens inserted 4.5 and 5 mm above the base of the corolla-tube, the staminode obsolete; ovary oblong-subobovate, glabrous; fruiting-calyx tough, the tube to 4 mm long, densely long-pubescent, the lobes firm and stiff, to 22 mm long and 7 mm wide, divergent and the calycinal crest callose, converging inwards.

In thickets and dry forests from Cuba and northern Mexico to Panama. This species is introduced and naturalized in India, China, Java, and elsewhere in the Old World tropics and is widely cultivated.

"Purple-wreath" (English), "adelfa," "adolfina," "choreque," "estrella azul," "flor de Jesús," "flor de Santa María," "hoja chigüe," "lengua de vaca," "raspa-sombrero," "soltero," and "totopostillo."

CANAL ZONE: Barro Colorado Island, *Aviles 14* (BARRO). Ahorca Lagarto to Culebra, *Cowell 374* (NY, US). Barro Colorado Island, *Shattuck 412* (BARRO, part).

3a. **Petrea volubilis** var. **pubescens** Moldenke, Feddes Repert. 43: 45. 1938.

P. mexicana H.B.K. *ex* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 329. 1844.

This variety differs from the typical variety in its leaf-blades which are conspicuously pubescent on both surfaces when young or only beneath when mature.

The variety occurs from Mexico to Panama in habitats similar to those of the typical variety. It is also cultivated.

VERAGUAS: Without locality, *Warscewicz 10* (B), *Warscewicz 11* (G).

8. DURANTA

Duranta L., Sp. Pl., 637. 1753; Gen. Pl., ed. 5. 284. 1754.

Castorea Mill., Gard. Dict., abridg. ed. 4. 1754.
Ellisia P. Browne, Civ. Nat. Hist. Jamaica 262. 1756.
Hoffmannia Loefl., Iter Hisp. 194. 1758.
Darbyana A. M. Murray, Letters 305, in text. 1856.

Glabrous or pubescent, often spinose *shrubs*. Leaves decussate-opposite or whorled, simple, entire or dentate, deciduous. *Inflorescences* mostly terminal, rarely axillary or abbreviated, indeterminate, racemiform, elongate. *Flowers* often showy, mostly pedicellate, each borne in the axil of a small bractlet; calyx gamosepalous, subplicate, tubular or subcampanulate, 5-costate, mostly truncate apically, each rib terminating in a short subulate tooth, the posterior tooth smallest; corolla gamopetalous, hypocrateriform, mostly blue, purple, or white, the tube cylindric, straight or curved above, exserted from the calyx, the limb spreading, regular or oblique, 5-parted, mostly pubescent at the mouth, the lobes rounded, usually unequal, mostly pubescent on the inner surface; stamens 4, didynamous, included, inserted at or above the middle of the corolla-tube; filaments very short; anthers sagittate, dorsifixed, erect, with parallel thecae; style terminal, shorter than or equaling the lower stamens, the stigma obliquely subcapitate, very shortly and unequally 4-lobed; ovary more or less completely 8-celled, composed of 4, 2-celled carpels, each cell 1-ovulate; fruiting-calyx accrescent, flask-shaped, usually surpassing and closely appressed to the fruit, but not coalesced with it, usually coarctate-rostrate at the apex. *Fruit* drupaceous, mostly completely included in the mature calyx, the exocarp fleshy, the endocarp hard; pyrenes 4, each 2-celled and 2-seeded.

A genus of 50 species and infraspecific entities, widespread in subtropical and tropical America, ranging from Florida and Bermuda through the West Indies, Mexico, and Central America to Argentina. One species is doubtfully native in

Thailand. The genus is widely cultivated and frequently naturalized in tropical parts of the Old World.

a. Leaf-blades pubescent beneath, thick-textured; branchlets densely tomentose ..... 1. *D. costaricensis*
aa. Leaf-blades glabrate beneath, mostly thin-textured; branchlets usually glabrate.
  b. Corolla blue to lilac, violet, or purple.
    c. Mature leaf-blades mostly 1.5–5 cm long ..... 2. *D. repens*
    cc. Mature leaf-blades mostly less than 1.5 cm long ..... 2a. *D. repens* var. *microphylla*
  bb. Corolla white ..... 2b. *D. repens* var. *alba*

1. **Duranta costaricensis** (Donn. Sm.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1005. 1938.—FIG. 8.

D. repens γ *mutisii* 3. *acuminata* Kuntze, Rev. Gen. Pl. 2: 507. 1891.
D. mutisii var. *costaricensis* Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 9. 1895.

Shrub or *tree*, 2–15 m tall, *or* thorny *liana*; stems and older branches sometimes armed; branches long, arching, densely short-pilose, mostly unarmed at the flowering tips; branchlets slender or stout, often spinose, obtusely tetragonal, densely tomentose with short and appressed yellowish tomentum, glabrate in age; spines borne in opposite or subopposite pairs just above the leaf-axils, divergent, 5–10 mm long, stout, and ampliate basally, very sharp-pointed, sometimes slightly recurved at the apex; leaf-scars usually borne on definitely raised sterigmata ca. 1 mm long. *Leaves* opposite, subopposite, or ternate, elliptic or lanceolate-elliptic to lanceolate or ovate-lanceolate, 3–8.5 cm long, 1.1–4.5 cm wide, apically acute or subacuminate to narrowly long-acuminate, basally acute or acuminate to obtuse, the margin entire or subentire to distinctly serrulate near the middle or above but not to the apex, often subrevolute, firmly chartaceous or subcoriaceous, dark-green and very shiny above, somewhat lighter beneath, often nigrescent in drying, above tomentose-pubescent along the larger veins and occasionally on the lamina or only obscurely puberulous, glabrescent in age, densely to lightly short-pubescent beneath, especially along the venation or toward the base of the blade, midrib and secondary veins impressed above, sharply prominent beneath, prominently joined in many loops near the margins beneath; petioles slender, 5–17 mm long, varying from densely spreading-pubescent or tomentose when young to sparsely scattered pilose in age, the hairs ochraceous. *Inflorescences* axillary and terminal, 2 or 3 per upper node, abundant at the ends of the branchlets, racemose, nutant, racemes many-flowered, mostly simple, widely spreading, 5–13 cm long and 1–2.5 cm wide, the axillary racemes becoming 20 cm long in fruit, the terminal raceme elongating to 30 cm; peduncles 1–3 cm long, the rachis slender, densely ochraceous-pubescent or sordid-tomentose like the branchlets, occasionally with 1 or 2 pairs of short branches 3–6 cm long near the base, each subtended by a pair of large foliaceous bracts resembling the leaves but only 1–4 cm long and 4–15 mm wide, foliaceous bractlets, subtending each pedicel, 5–8 mm long, 2–3 mm wide, long-acuminate apically, often persisting in fruit; pedicels slender, 1–4 mm long becoming to 10 mm long in fruit, densely yellowish-tomentose; calyx tubular, 6–8 mm long and 4 mm wide, densely short pubescent or pilose, 5-costate, lighter between the ribs toward the apex, the rim distinctly 5-toothed, the teeth long and slender, subulate-tipped; corolla hypocrateriform, bluish or lavender to light-

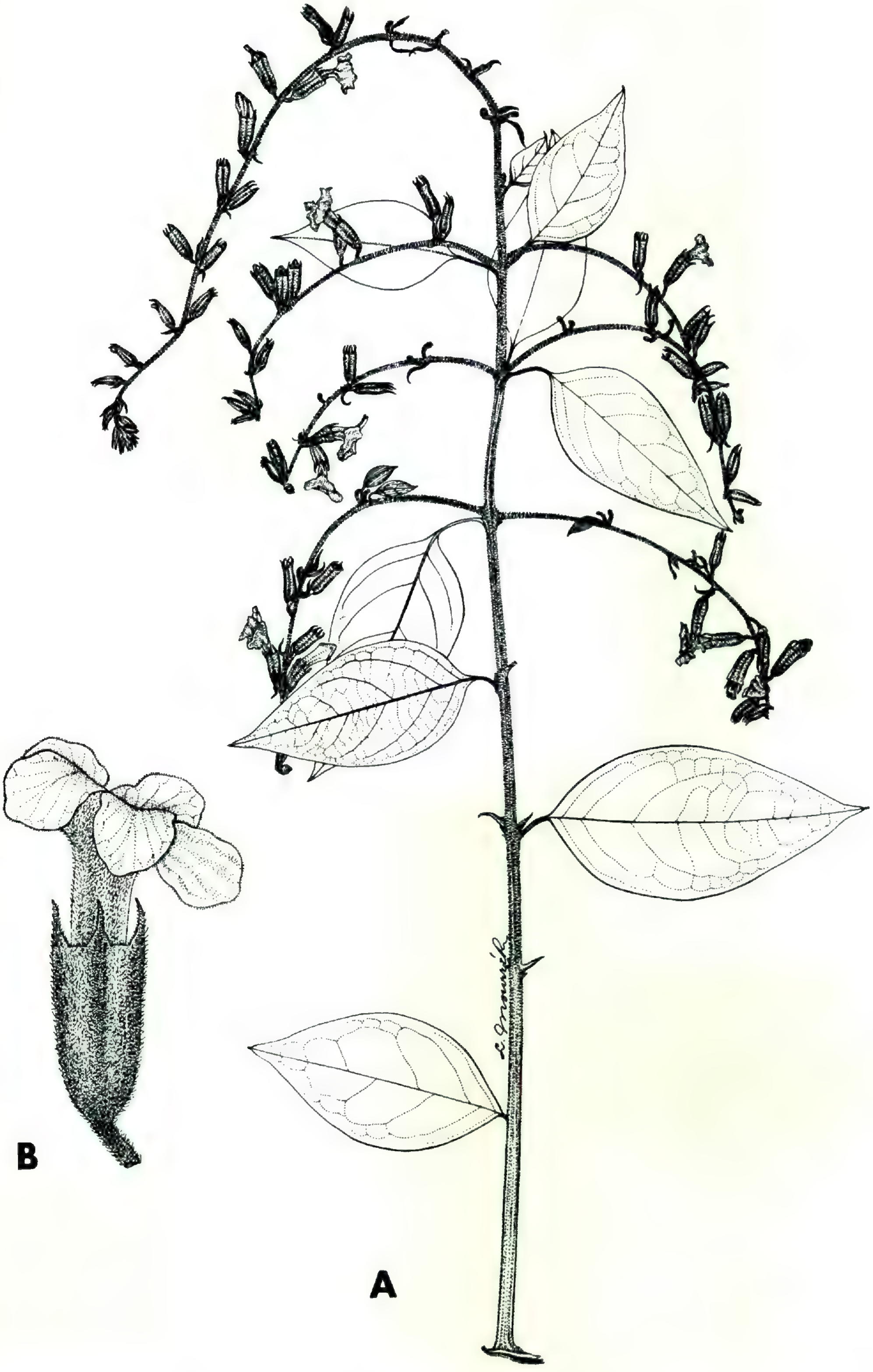

FIGURE 8. *Duranta costaricensis* (Donn. Sm.) Standl.—A. Habit (× ⅝).—B. Flower (× 3). [After *Allen 1551* (MO).]

purple or white, ca. 1.5 cm long, puberulent; fruiting-calyx obvolute, puberulent or eventually glabrate. *Fruit* pale-yellow or orange, ca. 1 cm long and wide.

In thickets and moist forests and along trailsides, mostly at high altitudes, Costa Rica and Panama.

Known as "uña de gato."

CHIRIQUÍ: Trail from Bambito to Cerro Punta, 1400–2300 m, *Allen 320* (F, MO, NY). Llanos on slopes of Volcán de Chiriquí and along Río Chiriquí Viejo, 1200 m, *Allen 990* (MO). Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1476* (MO, NY). Chiquero, Boquete District, 5500 ft, *Davidson 553* (F, MO). Valley of the Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9068* (BMIC, MO). Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9074* (MOLDENKE); Boquete, Finca Collins, at edge of forest, 6000 ft, *Ebinger 739* (MO, US). Between El Hato (Volcán) and Cerro Punta, llanos, *Ebinger 798* (MO). One mi. S of Volcán, 900 m, *Graham 303* (MICH). Valley N of Bajo Lino, 3500 ft, *Bro. Maurice 851* (US). Río Chiriquí Viejo valley between El Volcán and Cerro Punta, *White 9* (MO, NY). Near Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 590* (MO). Without locality, *Allen 1551* (MO).

2. **Duranta repens** L., Sp. Pl. 637. 1753.

D. erecta L., loc. cit. 1753.
D. ellisia Jacq., Enum. Pl. Carib. 26. 1760.
D. plumieri Jacq., Select. Stirp. Amer. Hist. 186, *t. 176, fig. 76.* 1763.
D. racemosa Mill., Gard. Dict., ed. 8. 1768.
D. angustifolia Salisb., Prodr. 108. 1796.
D. latifolia Salisb., Prodr. 108. 1796.
D. dentata Rich. *ex* Pers., Syn. Pl. 2: 142. 1806.
D. xalapensis H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 206. 1817.
D. plumieri var. *strigillosa* Schau. *in* Mart., Fl. Bras. 9: 271. 1851.
Darbyana integrifolia A. M. Murray, Letters 306. 1856.
Duranta bonardi Guillard *ex* Bocq., Adansonia 2: 112. 1862.
D. plumieri var. *ellisia* (L.) Hort. *ex* Woodrow, Gardening Ind. 420. 1889.
D. plumieri var. *glabra* Hieron *ex* Niederl., Bol. Mens. Mus. Prod. Argent. 3(31): 322. 1890.
D. repens α *multidentata* Kuntze, Rev. Gen. Pl. 2: 507. 1891.
D. repens β *paucidentata* Kuntze, loc. cit. 1891.
D. repens γ *mutisii* 1. *acuta* (L.) Kuntze, loc. cit. 1891.
D. repens γ *mutisii* 3. *acuminata* (a) *glabrifolia* Kuntze, loc. cit. 1891.
D. rostrata Hort. *ex* Wehmer, Pflanzenst., ed. 2. 2: 1023. 1931.
D. spinosa Mill. *ex* Crevost & Pételot, Bull. Econ. Indo-chine 37: 1289. 1934.
D. macrophylla Bose, Hand Book Shrubs 46, 107, 122, & 123. 1965.

An extremely variable and polymorphic *shrub* or small *tree* to 7 m tall; branches slender, arching, often drooping or trailing, unarmed or spiny, sometimes scandent or semi-scandent, usually glabrate, sometimes obscurely appressed-strigillose; branchlets tetragonal. Leaves opposite, numerous, very variable in shape, size and texture, ovate-elliptic or ovate to obovate, 1.5–5 cm long, 1–4 cm wide, apically obtuse or acute to acuminate or apiculate, basally cuneate into the petiole at base, margins entire or coarsely serrate above the middle, occasionally coarsely dentate throughout (especially on sterile shoots), mostly thin-textured, often almost membranous, glabrate on both surfaces; petioles slender, 1–8 mm long. *Inflorescences* racemose, terminal and axillary, usually concentrated at or near the tips of the branches, loosely many-flowered, erect or usually recurved, often paniculate, 5–30 cm long, bractlets minute, occasionally subfoliaceous; pedicels 1–5 mm long. *Flowers* sweet-scented with the odor of vanilla; calyx tubular, 3–4.5 mm long, angled, appressed-strigillose, sometimes decidedly canes-

cent, the teeth minute, basally triangular, apically subulate for ca. 1 mm or less; corolla hypocrateriform, blue, lilac, violet, or light violet-blue to lavender or purple, sometimes mauve or purplish with a white tube and with or without two purplish stripes in the tube, the tube surpassing the calyx by 2–3 mm, densely puberulent outside above the calyx, the limb 7–9 mm wide, densely puberulent on both surfaces, especially outside and toward the throat within, the puberulence often canescent in bud; fruiting-calyx accrescent, yellowish, glabrous, shiny, prolonged into a curved beak beyond the fruit. *Fruit* yellow or orange-yellow, globose, 7–11 mm in diameter, completely enclosed by the fruiting-calyx.

In woods, thickets, hedges, fencerows, and roadsides throughout subtropical and tropical America from Florida, Texas, and southern California to Argentina; introduced and often naturalized in many parts of tropical Africa and Asia, Australia, and Oceania; widely cultivated in all warm portions of the civilized world.

"Golden dewdrop," "heliotrope bush," "pigeon-berry," and "skyflower" (English), "adonis morado," "celosa cimarrona," "cuenta de oro," "espina de paloma," "fruta de iguana," "lora."

Some of the infraspecific names proposed may be worth maintaining, but more study is needed to validate their separation.

BOCAS DEL TORO: Colón Island, *von Wedel 36* (MO, NY). SW of Bocas at Maccaw Hill, Colón Island, 0–120 m, *von Wedel 563* (MO). CANAL ZONE: *Blum & Tyson 2067* (MO). Cultivated, Colón, *Moldenke 19802* (NY). Near Panamá, *Sargent 40* (AAH, US). Lawn shrub, Parsons Street, Diablo Heights, *Welch 19849* (UC). CHIRIQUÍ: 1½ mi. from Boquete on highway toward David, *Dwyer & Hayden 7631* (MO). Forests around El Boquete, 1000–1300 m, *Pittier 3328* (NY, US). Near San Félix, eastern Chiriquí, 0–120 m, *Pittier 5438* (F, NY, US). Llanos Francia, 3300 ft, near Boquete, *Stern et al. 1201* (BM, MO). Near Bouquete, 1200–1500 m, *Woodson & Schery 792* (MO, NY). COCLÉ: Near La Pintada, 300 m, *Allen 3607* (MO, NY). Llanos outside of town, *Ebinger 1034* (MO). Near El Valle de Antón 500–700 m, *Seibert 433* (NY, NY). LOS SANTOS: Between Los Santos and Guararé, *Woodson, Allen, & Seibert 1199* (MO, NY, NY). PANAMÁ: Panamá Vieja, *Duke 5714* (MO). Panamá, *Halsted s.n.* (NY). Roadside, Old Panamá, *Killip 3395* (US). Common near beach, E of Bella Vista, *Maxon & Valentine 6930* (NY, US). Cultivated, Panama City, *Moldenke 1224* (AAU). Panamá, *Bro. Nicolas s.n.* (US). Savannas, Panamá, *Bro. Paul 249* (US). Savannas N of Panama City, *Bro. Paul 438* (NY). Panamá, *Seemann 356* (S). Near San Carlos, *Woodson et al. 1698* (MO, NY, NY). Coastal thicket, Bella Vista, *Standley 25309* (US). In thicket, Nuevo San Francisco, *Standley 30704, 30732* (both US).

2a. **Duranta repens** var. **microphylla** (Desf.) Moldenke, Phytologia 1: 483. 1941.

D. microphylla Willd. *ex* Schlecht., Enum. Hort. Berol. Suppl. 43. 1813, nom. nud.
D. microphylla Desf., Cat. Hort. Paris, ed. 3. 392. 1829.

This variety differs from the typical variety in its mature leaf-blades being mostly or uniformly less than 1.5 cm in length.

The variety is known from Panama and the Galapagos Islands as well as from cultivated material from Trinidad and France. It seems more distinct than most of the other infraspecific taxa proposed in *Duranta repens*. Some of the cultivated material probably represents var. *grandiflora* Moldenke, but this is difficult to determine from dried material.

PANAMÁ: Outskirts of woods near Panamá, *Hayes 68* (BR).

2b. **Duranta repens** var. **alba** (Masters) Bailey *ex* Bailey & Bailey, Hortus 225. 1930.

D. plumieri var. *alba* Masters, Gard. Chron. 63 [ser. 3, 3:]: 44, *fig.* 9. 1888.
D. repens fo. *alba* Matuda, Amer. Midl. Naturalist 44: 576. 1950, hyponym.
D. erecta var. *alba* (Masters) Caro, Revist. Argent. Agron. 23: 11. 1956.

This variety differs from the typical variety in its white corollas.

The variety occurs sporadically throughout the range of the species and is widely cultivated in subtropical and tropical regions, sometimes escaping.

"Adonis blanco," "heliotropio blanco," "no-me-oluides," "varita de San Jose," "white skyflower."

PANAMÁ: Cultivated, Panama City, *Moldenke 1223* (AAU). Juan Díaz, *Standley 30534* (US).

9. CITHAREXYLUM

Citharexylum L., Sp. Pl. 625. 1753, Gen. Pl., ed. 5. 273, as "*Citharexylon*." 1754.

Rauwolfia Ruiz & Pav., Fl. Peru. 2: 26, *pl. 152*. 1799, non *Rauvolfia* L., Gen. Pl., ed. 5. 1754.
Scleroon Benth. *ex* Lindl., Bot. Reg. 29: Misc. 65–66. 1843.
Cacocalyx S. Wats., Proc. Amer. Acad. Arts 24: 67. 1889.

Trees or *shrubs*, rarely climbing; branches and branchlets usually tetragonal, sometimes spiny; leaf-scars mostly large, corky, and elevated, borne on more or less prominent sterigmata. *Leaves* deciduous, decussate-opposite, ternate, or verticillate, rarely approximate, subopposite, or even alternate, entire or dentate, usually bearing a pair of prominent glands at the base of the blade, petiolate or sessile, the petioles rarely myrmecophilous at the apex; exstipulate. *Inflorescence* axillary and terminal, indeterminate, racemiform or spicate, mostly simple, occasionally sparsely branched, mostly elongate and many-flowered, rarely reduced to only a few flowers, erect or nutant; each subtended by a usually tiny and inconspicuous bractlet. *Flowers* small; calyx tubular or cyathiform, regular or somewhat zygomorphic, thin, accrescent, apically truncate and entire or 5-toothed or -lobed; corolla infundibular or hypocrateriform, mostly yellow or white, varying to blue, violet, or lilac, the tube narrow-cylindric and regular, the limb spreading, usually 5-parted, rarely 4- or 6-parted, with broad, slightly irregular lobes, the 2 hindmost outermost in prefloration, mostly more or less pubescent in the throat; stamens 4, mostly didynamous, inserted at or above the middle of the corolla-tube, included, a fifth stamen represented by a rudimentary staminode, or occasionally stamens 5 or even 6, the filaments very short, the anthers ovate or sagittate, introrse, erect, with 2 parallel thecae opening by longitudinal slits and with a thickened connective which often surpasses the thecae in length; style terminal, included, often thickened upwards, the stigma shortly bifid, ovary perfectly or imperfectly 4-celled, 2-carpellate, each cell with 1 lateral anatropous ovule. *Fruit* drupaceous, with a juicy exocarp and hard endocarp, the 2 pyrenes 2-celled and 2-seeded, often separated by a median fissure; the fruiting-calyx conspicuously enlarged and indurated, cupuliform or patelliform, shorter than the fruit.

A genus of 139 species and infraspecific taxa, ranging from Bermuda, Florida, and Texas through Mexico, Central America, and the West Indies to Argentina

and Uruguay. Many species are cultivated for ornament in various parts of the Old and New Worlds. Several fossil forms are known from the Tertiary of the United States, Colombia, and Italy.

a. Leaves ternate or alternate ..... 1. *C. macrochlamys*
aa. Leaves decussate-opposite or approximate.
  b. Leaf-blades glabrous or subglabrate beneath when mature.
    c. Veins and veinlets numerous, the reticulation more or less conspicuous and prominulous, at least above when dry ..... 2. *C. donnell-smithii*
    cc. Veins and veinlets sparse, the reticulation usually more or less obscure on both leaf-surfaces when dry.
      d. Leaf-blades mostly blunt, obtuse, or only subacute at the apex; basal prolongation folded over to enclose a pair of elongate dark glands ..... 3. *C. caudatum*
      dd. Leaf-blades distinctly acute or acuminate at the apex, the base not plainly invaginated to enclose the glands.
        e. Leaf-blades with a basal pair of large, prominent, and conspicuous heavy black glands to 4 mm long ..... 4. *C. macradenium*
        ee. Leaf-blades with only a few basal small appressed and inconspicuous glandular disks ..... 5. *C. recurvatum*
  bb. Leaf-blades distinctly hairy beneath.
    f. Flowers sessile or subsessile; leaf pubescence simple.
      g. Leaf-blades subglabrate, pulverulent, or merely puberulent on the lamina beneath, more or less dichotomously short-pubescent only along the midrib ..... 6. *C. viride*
      gg. Leaf-blades velutinous on the entire surface beneath ..... 7. *C. cooperi*
    ff. Flowers distinctly pedicellate; leaf-blades densely furfuraceous-tomentose beneath with many-branched hairs ..... 8. *C. lankesteri*

1. **Citharexylum macrochlamys** Pittier, Contr. U. S. Natl. Herb. 18: 254. 1917.

C. macranthum Pittier, Contr. U. S. Natl. Herb. 18: 169. 1916, non *Citharexylon macranthum* Hayek, Bot. Jahrb. Syst. 42: 170. 1908.

Tree, to 30 m tall; trunk straight, to 50 cm diameter basally, the bark reddish rugose, the core dirty-white; wood hard and tough; crown elongate, and the limbs slightly ascending; branchlets and twigs stout, more or less fistulose, acutely tetragonal or 6-angled, slightly 4–6 margined, light-brown, glabrous; leaf-scars comparatively large, oblong, ca. 5 mm long and 3 mm wide, sessile or borne on extremely short sterigmata, most prominent at the base. *Leaves* usually alternate, ternate at the ends of the young flowering shoots; elliptic-oblong or elliptic to ovate or subobovate, entire but often undulate in drying, 9.8–25 cm long, 5.5–9.2 cm wide, apically acute or subacute to acuminate or rounded, basally subtruncate to acute or rounded-attenuate or even cuneate with 2 or 3 large, thickened, black glands beneath and parallel to the petiole, thin-chartaceous or membranous, bright-green on both surfaces, whitish beneath when immature, obsoletely puberulent on both surfaces, especially beneath, or glabrous, smooth to the touch above, finely reticulate-roughened between the salient veins beneath; petioles slender or stout, 1.5–3.7 cm long, more or less broadly sulcate above, basally greatly ampliate in the form of a shield, densely but minutely puberulent or glabrate. *Inflorescence* subterminal, the racemes usually ternate, simple, mostly erect or ascending axillary in the 2 or 3 upper nodes of the branchlets, 13–28 cm long, 1–2 cm wide, loosely many-flowered; peduncles slender or stout, 4–7.5 cm long, minutely puberulent or glabrate; rachis glabrous to minutely hirsute or puberulous; pedicels slender, 0.5–1.5 mm long, puberulent or minutely hirtellous; bracts and bractlets absent;

prophylls setaceous, ca. 1 mm long. *Flowers* distinctly zygomorphic, large for the genus, ca. 17 mm long; calyx salverform, ca. 5 mm long, glabrate or finely pubescent, apically irregularly 5-dentate; corolla white, hypocrateriform, 15.5–17 mm long, the tube cyclindric, slightly arcuate, ca. 11 mm long, the limb broad, the lobes well developed, the median lobe irregularly rounded-acuminate with a narrow claw, the lateral lobes elongate, conchiform and obtusely pointed apically; stamens included, inserted well below the middle of the corolla-tube, glabrous, the filaments slender, the anthers elliptic, basally emarginate, apically rounded; pistil entirely glabrous, the style 1–1.5 mm long, the stigma capitellate, faintly bilobed, papillose, the ovary ovoid, 4-celled, each cell 1-ovulate.

In wet forest and thickets, Panama and Colombia.

Closely related to *Citharexylum macrophyllum* Poir. of northern South America.

COLÓN: High forest along the Río Fató, above Nombre de Dios, 10–100 m, *Pittier* 3897 (GH, NY, US). Forests or thickets, Río Fató, *Pittier 4199* (BM, NY, US). DARIÉN: Río Balsa, between Manene and Tusijuana, *Duke 13550* (BMIC).

2. **Citharexylum donnell-smithii** Greenm. *in* Donn. Sm., Enum. Pl. Guatem. 7: 70. 1905, hyponym; Greenm., Publ. Field Columbian Mus. Bot. Ser. 2: 186. 1907.

C. ghiesbreghtii Moldenke, Phytologia 1: 413. 1940.

Tree or *shrub* 1–20 m tall; crown broad and dense; trunk to 76 cm in diameter basally; bark dark gray-brown or nearly black, furrowed and roughened in age; branchlets and twigs slender, acutely or obtusely tetragonal, buff or brownish, often dark, striate and more or less lenticellate, sparsely strigillose to glabrous, more or less shiny; nodes somewhat ampliate, often oblique; leaf-scars large, borne on short, conspicuous sterigmata. *Leaves* opposite or approximate with internodes to 1 cm long between members of a pair, lanceolate or oblong-lanceolate to elliptic, 4.5–21 cm long, 2.1–6.5 cm wide, apically acuminate attenuate or subacuminate (rarely obtuse or emarginate on stunted leaves), entire or rarely with a few, short, acute teeth near the apex, basally acute or cuneate with 1–3 pairs of small discoid or oblong glands, glabrous and sometimes sparsely punctate on both surfaces, chartaceous or thin-chartaceous, firm, when fresh uniformly bright- or dark-green on both surfaces or rich-green above and paler beneath, the midrib sometimes sparsely and minutely strigillose-puberulent above; petioles slender or stout, 1–2.5 cm long, not ampliate at the base, glabrous or sparsely and obscurely pulverulent-puberulent. *Racemes* numerous in the uppermost leaf-axils or terminal, often crowded at the tips of the branchlets, elongate, 10–45 cm long, 1–1.8 cm wide, simple or occasionally with 1–3 pairs of lateral branches to ca. 10 cm long, densely many-flowered, recurved and nutant or pendent; peduncles slender, 1.5–6 cm long, glabrous or sparsely strigillose; rachis slender, glabrous; pedicels slender, spreading, 1–3.5 mm long, becoming 6 mm in fruit, glabrous or sparsely strigillose; bractlets few, linear, to 5 mm long, glabrate; prophylls sessile setaceous, to 1–2 mm long. *Flowers* very fragrant, calyx campanulate or tubular-campanulate, 2–3 mm long, ca. 2 mm wide, strongly 5-angled in cross-section, sinuately 5-dentate and ciliolate apically, glabrous except for the puberulent apex;

corolla white, yellowish-white or greenish-white to cream-color or creamy-buff, tubular-campanulate, usually about twice as long as the calyx, 5–8 mm long, the tube more greenish-white than the limb, glabrous outside, pubescent within, the limb ca. 5 mm wide, 5-lobed, the lobes sub-equal spreading, sub-equal ca. 2 mm long, oblong, rounded, pubescent within, glabrous outside; stamens slightly exserted; style and ovary glabrous; fruiting-calyx campanulate, herbaceous, to 3 mm long and 5 mm wide, glabrous, its rim spreading, subentire or more or less obscurely 5-apiculate, becoming obtusely 5-lobed or -split in age. *Fruit* orange to reddish or pale-reddish and very showy when fresh, drying black or purplish-black to bluish and wrinkled, oblong or oblong-spherical, 2-lobed, 6–7 mm long, ca. 6 mm wide, glabrous, extremely shiny, fleshy; pyrenes sub-meniscoidal, 5–6 mm long, 3–3.5 mm wide, smooth.

In forests and pastures, on brushy slopes and roadsides, cafetales, potreros, and quebradas, ranging from southern Mexico to Panama. The fruit is a favorite food of wild pigeons.

"Buena noche," "cola de pava," "coral negro," "cordoncillo," "damas," "moca de pava," "palo paloma," "paraiso," "seguilla," and "uva."

CHIRIQUÍ: Very common in potreros, near Finca Lerida, 5500 ft, *Allen 4730* (MO, NY). Bajo Mono, Boquete District, 4500 ft, *Davidson 483* (F, MO). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 899* (MO). Valley of Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9057* (BMIC). Mixed evergreen forest, 5.5 mi. S of Cerro Punta, along cleared path in forest, 1700 m, *Graham 281* (MICH). On way to Lérida (Boquete), *Bro. Maurice 885* (MO). Near Boquete, Finca Collins, "El Velo," 6150 ft, *Stern et al. 1969* (MICH, MO, US). Pasture Río Chiriquí Viejo valley near El Volcán, *White 214* (F, MO). Near Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 870* (MO, NY).

3. **Citharexylum caudatum** L., Sp. Pl., ed. 2. 2: 872, as "*Citharexylon*." 1763.—FIG. 9.

C. album Mill., Gard. Dict., ed. 8, no. 2. 1768.
Citharexylon erectum Sw., Prodr. Veg. Ind. Occ. 91. 1788.
C. berterii Spreng. *in* L., Syst. Veg., ed. 16. 2: 763. 825.
Citharexylum surrectum Griseb., Fl. Brit. W. Ind. Is. 497, pro parte. 1861.
C. lindenii Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 208. 1863.

Open, graceful *shrub* or small, slender, straggling, rounded *tree* to 20 m tall, occasionally vine-like; stems to 20 inches d.b.h.; bark white; branches and branchlets tetragonal or subterete, often striate, glabrous, brownish, or the young shoots drying dark; leaf-scars large, borne on corky large sterigmata. *Leaves* opposite, lanceolate or oblong to narrowly elliptic, 4–17.5 cm long, 2.4–7.7 cm wide, apically blunt or subacute, rarely apiculate or emarginate, entire, cuneately narrowed to the base, the margins recurved to enclose a pair of elongate dark basal glands, firmly chartaceous or subcoriaceous, dark-green and shiny above, lighter and shiny and punctate beneath, glabrous on both surfaces, the midrib often orange-brown above and light-brown or pale greenish-white beneath and (when fresh) suffused below with buff, minor venation delicate, sparse, often obscure; petioles 0.3–2.4 cm long, glabrous. *Racemes* axillary or terminating axillary branchlets, erect or pendent, 3–38 cm long, 1–1.5 cm wide, densely many-flowered, unbranched or rarely furcate; peduncles slender, 0.5–4.5 cm long, glabrate; rachis slender, grass-green, glabrate or glabrous; pedicels slender, 1–2.5 mm long,

FIGURE 9. *Citharexylum caudatum* L., habit (× ⅝). [After *von Wedel 1146* (MO).]

glabrate; bracts occasionally present, foliaceous, lanceolate, to 2.5 cm long and 1 cm wide, glabrous on both surfaces; prophylls setaceous, 1–2 mm long, glabrate. *Flowers* fragrant; calyx campanulate or cyathiform, 3–4.5 mm long, mostly glabrate outside, the tube pale-green, apically subtruncate, minutely apiculate or obsoletely 5-repand-dentate, obscurely ciliate; corolla white or cream-colored,

5–8 mm long, infundibular, the tube about twice as long as the calyx, tomentose apically, villous at the throat, the limb 5-lobed, 4–5 mm wide, lobed ⅓–⅔ of its length, the lobes obovate, the filaments ca. 0.5 mm long, the anthers ca. 1 mm long, the staminode rudimentary; pistil ca. 3.5 mm long, the style ca. 2 mm long, stigma bilobed, ovary obovate. *Fruit* reddish-green or yellow to orange or red, finally shiny black when mature and in drying, oblong or globose-oblong to obovate or subglobose, 6–12 mm long, 5–10 mm wide, glabrous, pyrenes 1-celled; fruiting-pedicels to 3 mm long; fruiting-calyx cupuliform or eventually patelliform, herbaceous or indurated, to 3 mm long and 4 mm wide, 5-angled, glabrous, apically subtruncate, 5-apiculate or eventually splitting irregularly and erose.

In forests and thickets, hammocks and pastures, on brushy slopes and hillsides, in swamps and on beaches, ranging from the Bahamas and Mexico through the West Indies and Central America to Colombia and Peru. This species is introduced on Guam, and it is cultivated for ornament elsewhere. It is a very variable species.

"Wild cherry," "white fiddlewood," "fiddlewood" (English), "bois carré," "canilla de venado," "coffé marron," "dama," "guayo blanco," "palo de dama," "palo guitarre," "penda," "pendola de sierra," "roble amarallo," "roble blanco."

BOCAS DEL TORO: Flat Rock, region of Almirante, *Cooper 561* (F, S, US, YU). Changuinola Valley, *Cooper & Slater 139* (F, US, YU); *Dunlap 528* (F, US); *von Wedel 261* (MO). Water Valley, *von Wedel 775, 805* (both MO). Near Chiriquí Lagoon, *von Wedel 1058, 1146, 1158* (all MO). Lagoon, Water Valley, near Chiriquí Lagoon, *von Wedel 1484* (MO). Chiriquí Lagoon, Old Bank Island, *von Wedel 2028* (MO). Chiriquí Lagoon, Isla Colón, *von Wedel 2469* (MO, NY). Shepherd Island, Chiriquí Lagoon, *von Wedel 2725* (MO). Western River, Chiriquí Lagoon, *von Wedel 2778* (MO). Careening Cay, Chiriquí Lagoon, *von Wedel 2812* (MO, NY). CANAL ZONE: Near Fort Sherman, *Bailey & Bailey 682* (BH, F). Ancon Hill, *Bartlett & Lasser 16308, 16314* (both MICH). Chagres, *Fendler 290* (GH, K, MO, NY, US). Margin of woods near seashore, Chagres, *Fendler 290b* (GH, K, US). Ancon Hill, *Gillespie P.8* (DS, S); *Piper 5562* (US); *Rowlee & Rowlee 397* (US). Between France Field and Cativa1, *Standley 30163* (US). Aspinwall, *Hayes 568* (BM, K). Ancon Hill, *Killip 12105* (US). Moist woods, Ancon Hill, *Standley 25178* (AAH, US). Moist forest, Ancon Hill, *Standley 26394* (AAH, US). Near Fort Sherman, *Standley 31195* (US). France Field, *Stevens 171, 979* (both ILL). Sherman to Sweetwater, *Stevens 1039* (ILL). Near Corozal, *Allen 1836* (F, MICH, MO). Matachin, *Cowell 195* (NY). Colón to Empire, Panama Railroad, *Crawford 397* (NY, PH). Rocky slopes on Interamerican Highway 4 mi. NW of Bejuco and Ancon Hill, *Duke 4598* (MO). Near Galena Point, *Dwyer & Robyns 151* (MO). Aspinwall, *Hayes 889* (NY). In government forest along Las Cruces Trail, 75 m, *Hunter & Allen 705* (MO). In government forest along Las Cruces Trail, 75 m, *Hunter & Allen 720* (MO). Ancon Hill, *Maxon 6775* (NY, US). Between Corozal and Ancón, 10–30 m, *Pittier 2631* (BM, F, GH, NY, US). Albrook Air Force Base, forest border, *Tyson 1109* (MO). Albrook Air Force Base on Beacon Hill, *Tyson 2034* (MO). Open sunlight, bank of Cocoli River near lighthouse, *White 161* (F, MO). Open very moist habitat near Miraflores Lake, *White 163* (F, MO). Río Cocoli opposite lighthouse, *White 101* (MO). Río Cocoli near lighthouse, *White 102* (F, MO). CHIRIQUÍ: Without locality, *Hart C² .117* (K). COCLÉ: Bog, El Valle, *Dwyer 815* (MO). Penonomé, *Dwyer 2025, 2035* (both MO). Penonomé and vicinity, 50–1000 ft, *Williams 373* (NY, US). COLÓN: Brackish soil at Colón, *Lehmann K.287* (K). In outdoor cultivation, Colón, *Moldenke 19801* (NY). Colón, *Debeaux 45* (W); *Debeaux 51* (P). Near Camp Piña, 25 m, *Allen 3597* (MO, NY, S, UC, US). On point just outside Fort Sherman, *Blum & Dwyer 390* (MO). Margarita near Colón, *Dwyer & Robyns 169* (MO). Along shore of beach, María Chiquita, *Ebinger 452* (MO). Chagres, *Fendler 290* (K); *Epplesheimer s.n.* (F); *Gillespie s.n.* (DS). Manzanilla Island, *Hayes 714* (NY). Colón, *Kuntze 1820* (NY). Beach and adjacent roadside, Nuevo Chagres, *Lewis et al. 1853* (BMIC, MO, US). Mangrove swamp, Colón, *Moldenke 1229* (AAU). Beach between Fató and Playa de Damas, *Pittier 3942* (GH, NY, US). PANAMÁ: Panamá, *Andersson s.n.* 1852 (S). Ancón, *Bro. Celestine 73* (US). Panamá,

Duchassaing, 1850 (LE); *Duchassaing*, 1851 (P); *Duke 4598* (UC). Rocky slope on Interamerican Highway 4 mi. NW of Bejuco, *Duke 4599* (UC). Road between Bodega Bay and Río Mata Puerco, San José Island, *Duke 12507* (MO). Occasional along shores, San José Island, *Erlanson 23* (DS, MICH, NY). Open scrub, San José Island, *Erlanson 310* (MICH, NY). Panamá, *Bro. Gervaisius 151* (US). San José Island, *Harlow 5* (US). Hill SW of camp, San José Island, *Johnston 228* (MO, US). Panama City, Bellevista, *Macbride 2738* (F, NY, US). Savannas N of Panama City, *Bro. Paul 389* (NY). Bella Vista, *Piper 5361* (NY, US). Panamá, *Seemann 522* (BM, K); *Standley 25916, 27742, 28171* (all US). Tumba Muerto Road near Panamá, *Standley 29754* (US). Panamá, *Standley 29781, 31882* (both US). SAN BLAS: Mulatuppu, *Duke 8548* (MO). Common near beach, Soskatupu Island, *Elias 1683* (BMIC, MO, US).

4. **Citharexylum macradenium** Greenm. *in* Donn. Sm., Enum. Pl. Guatem. 7: 70. 1905, hyponym; Greenm., Publ. Field Columbian Mus., Bot. Ser. 2: 188. 1907.

Tree, to 20 m tall with rounded crown; trunk to 25 cm in diameter at the base; bark gray, roughened by raised oblong strips; branchlets stout, acutely tetragonal, more or less 4-margined, light-gray, glabrous; twigs and young shoots slender, more or less acutely tetragonal, glabrous, shiny, drying dark; leaf-scars on short ascending sterigmata 1–3 mm long. *Leaves* opposite, or subopposite on vigorous shoots, easily detached from the stem, firmly chartaceous, entire, lanceolate or narrowly oblong to elliptic, 7–16.5 cm long, 1.7–4.2 cm wide, apically acute or short-acuminate, cuneately narrowed at the base, often infundibularly involute into the petiole and just above the base bearing (1–)2(–3) extremely large, thick, black glands to 4 mm long, one of which is often terminated by a discoid stigma-like body, bright-green on both surfaces, drying dark, glabrous and densely impressed-punctate on both surfaces, but not shiny, vein reticulation sparse, mostly obscure; petioles slender, 1.1–2.7 cm long, subterete or sulcate above, glabrous, nigrescent in drying. *Racemes* terminal 8.5–19.5 cm long, 1–1.5 cm wide, simple or with a pair of lateral branches near the base, densely many-flowered mostly erect, sometimes recurved; peduncles stout, 2–2.5 cm long, acutely tetragonal, glabrous, often with 1 or 2 bractlet-bearing nodes; rachis slender or stout, angled or ribbed, glabrous; pedicels slender, 1–1.5 mm long, glabrous, in fruit to 5 mm; bracts and bractlets caducous; prophylls setaceous, ca. 1 mm long. *Flowers* with the calyx cupuliform, ca. 2.5 mm long, 5-angled in cross-section, apically subtruncate, minutely 5-denticulate; corolla white, tubular-infundibular, the tube ca. 4 mm long, glabrate outside, pubescent in the throat, the lobes oblong, ca. 2 mm long, puberulent on both surfaces; style puberulent. *Fruit* lustrous, orange to orange-yellow or white, subglobose or round, 2-sulcate, 6–10 mm in diameter, fleshy when mature, bony when immature, glabrous; fruiting-calyx subpatelliform, ca. 2.5 mm long and 6 mm wide, 5-ribbed, glabrous, the rim irregularly and shallowly erose.

In cloud-forests of Costa Rica and Panama.

"Dama," "damas," or "danna."

CHIRIQUÍ: Dense woodland in cloud forest, Boquete, Cerro Horqueta, 5000–6000 ft, *Hayden 7077* (MOLDENKE). Dense woodland in cloud forest, Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7709* (LL). COCLÉ: Hills N of El Valle de Antón, near La Mesa, 1000 m, *Allen 2784* (MO, NY).

5. **Citharexylum recurvatum** Greenm., Publ. Field Columbian Mus. Bot. Ser. 2: 189. 1907.

Shrub or *tree* to 20 m tall; branchlets and twigs slender, brown, lenticellate, glabrous, mostly acutely or obtusely tetragonal, the branchlets sometimes terete; leaf-scars borne on stout ascending sterigmata to 4 mm long. *Leaves* opposite or approximate; firmly chartaceous, entire, oblong-lanceolate to almost ovate, 3.2–11.5 cm long, 1.4–3.7 cm wide, apically acute to obtuse, basally acute or abruptly acute and prolonged into the petiole, often subrevolute in drying, with a pair of small black glandular disks on the basal prolongation, above dark grayish-green, deeper green beneath, shiny, especially above, glabrous on both surfaces; minor veins slightly prominulous above, more or less obscure beneath; petioles stoutish, 1–1.5 cm long, glabrous, more or less margined to the base. *Racemes* terminal, 13–16 cm long, 1–1.8 cm wide, simple or paniculate, erect or nutant, densely many-flowered; peduncles and rachis slender, brown ribbed, glabrous, the peduncle 1–3.3 cm long; pedicels slender, 1–3 mm long, glabrous; bracts and bractlets absent; prophylls setaceous, ca. 1 mm long. *Flowers* small; calyx tubular-campanulate, ca. 3 mm long, glabrous, apically shallowly sinuate and minutely 5-denticulate; corolla-lobes subequal; style and ovary glabrous. *Fruit* at first yellow or orange, later shiny bluish-black, oblong, 5–7 mm long, ca. 5 mm wide, fleshy, glabrous, darkening and wrinkled in drying; pyrenes elliptic-oblong, 4–5 mm long, 3–3.5 mm wide, smooth; fruiting-calyx cupuliform, ca. 2.5 mm long and 5 mm wide, glabrous, shiny, ribbed, apically subtruncate or ultimately more or less scarious.

Known only from the type collection, which was collected in Costa Rica, and the two following collections.

CHIRIQUÍ: Finca Collins, near Boquete, *Blum & Dwyer 2577* (MO). PANAMÁ: Panamá, *Duchassaing s.n.* (GH).

6. **Citharexylum viride** Moldenke, Feddes Repert. 37: 238. 1934.

Shrub or *tree* to 2.5–7 m tall with a full spreading crown; trunk to 10 cm in diameter; branchlets and twigs slender, acutely tetragonal, light-brown, more or less ribbed, puberulent at the tips, glabrescent; leaf-scars borne on slender ascending or closely appressed sterigmata to 4 mm long. *Leaves* opposite or subopposite, entire, oblong-elliptic or rarely subobovate, 7–13 cm long and 2.8–5.8 cm wide, apically acute or acuminate, basally acute, chartaceous, uniformly bright-green on both surfaces, obscurely puberulent and glabrescent above, densely puberulent beneath and often distichously pubescent along the midrib, with 1 or 2 basal pairs of elongate brown glands beneath and parallel with the midrib, the midrib and secondary veins prominent above and beneath, secondary veins 5 or 6 pairs, ascending at ca. 45°, often not arcuate, minor venation abundant, prominulent on both surfaces; petioles slender or stout, 6–12 mm long, glabrate. *Racemes* axillary and terminal, 3–14 cm long, erect or nutant, simple or the terminal ones compound with 1–7 long branches, rather densely many-flowered; ca. 1.5 cm wide in fruit; peduncles and rachis slender or stoutish, brownish, densely puberulent, the peduncles 1–4 cm long, often nodose; bracts foliaceous, similar to the leaves but smaller; bractlets 4–8, linear, prophylls linear, 2–4 mm long linear. *Flowers*

fragrant; calyx campanulate, ca. 4 mm long and 2 mm wide, stramineous, lightly puberulent, deeply 4- or 5-toothed, somewhat 2-lipped, the teeth broadly triangular, ca. 2 mm long and wide, acute or obtuse, prominently striate-venose outside; corolla white, hypocrateriform, the tube equaling the calyx, the limb spreading, 4–5 mm wide, the lobes elliptic- or obovate-lingulate, ca. 2 mm long and wide, densely puberulent on both sides, the margins often crimped. *Fruit* oblong, ca. 7 mm long and 6 mm wide, slightly fleshy, glabrous, shiny, bright orange, drying wrinkled and brown or blackish and 2-sulcate; fruiting-pedicels dimorphic, some short and stout, ca. 1 mm long, others slender, elongate to 9 mm and often genuiflexuous apically, puberulent, white when fresh, the latter type often wanting; fruiting-calyx indurated, cupuliform, ca. 3.5 mm long and 5 mm wide, minutely puberulent or glabrate, usually borne on a corky receptacle, light-green, mostly 5-lobed with triangular lobes or merely erose.

In forest and second growth, on embankments, and along roadsides and streamsides, Costa Rica and Panama.

"Corrimiento" (Spanish) and "Wild lime" (English).

BOCAS DEL TORO: In cacao, region of Almirante, *Cooper III 384* (F, K, NY, US, YU). CHIRIQUÍ: Near Remedios, 0–150 m, *Allen 3661* (MO, NY). Progreso, *Cooper III & Slater 157* (AAH, F, GH, US, YU). Progreso, *Cooper III & Slater 201* (F, NY, US, YU). Embankment and streamside, Tolé, on the Transisthmian Highway ca. 50 mi. W of Santiago at Río San Pedro, *Dwyer & Hayden 7762* (MO). Changuinola, *Stork 42* (MICH, US). Roadside on the way to Miller's Hotel, Río Chiriquí Viejo valley near El Volcán, *White 223* (F, MO). Near Boquete, 1200–1500 m, *Woodson & Schery 755* (MO, NY). Without locality, *Wagner 580* (M).

7. **Citharexylum cooperi** Standl., Trop. Woods 10: 50. 1927.

Shrub or small *tree*, to 8 m tall with spreading crown; stems to 15 cm diameter; branchlets and twigs slender, acutely tetragonal, the young shoots light-brown, often 4-margined and more or less deeply sulcate on 2 opposite sides, short-pilose with spreading hairs, glabrescent; leaf-scars borne on conspicuous, stout, corky sterigmata. *Leaves* opposite; subcoriaceous (chartaceous or membranous when immature), entire, ovate or oblong to elliptic or oblong-elliptic, 4.8–20 cm long, 2.3–8 cm wide, apically acute or short-acuminate, basally acute or short-cuneate and decurrent with a pair of small discoid glands at the base (obscure or absent from mature leaves), pale gray-green and shiny above, usually brighter green beneath, glabrous or glabrate above, beneath velutinous overall, the midrib and secondary veins deeply impressed above and prominent beneath, minor venation sparse, more or less impressed or obscure above, prominulous beneath; petioles stout, 2–15 mm long, minutely puberulent or glabrate. *Racemes* numerous, erect, paniculate, terminal on short axillary twigs, 2–9 cm long, often with 1 or 2 pairs of branches at the base in the axils of bractlets, each branch to 1.5 cm wide, densely many-flowered; peduncles slender 1.5–3.5 cm long, short-pubescent, or canescent-puberulent or glabrate, usually with 1–5 nodes each bearing a pair of linear bractlets; rachis similar to the peduncles, mostly short-pubescent; pedicles filiform, to 2 mm long, pubescent or puberulent; bractlets linear, paired, to 5 mm long, short-pubescent or puberulent; prophylls setaceous, to 1 mm long. *Flowers* fragrant; calyx narrowly campanulate, ca. 4 mm long, sparsely hirtellous; corolla white, hypocrateriform, the tube ca. 2.5 mm long, the lobes ca. 2 mm long, obtuse,

minutely puberulent. *Fruit* orange, globose, ca. 8 mm long; fruiting-calyx much indurated and incrassate, ca. 4 mm long and 6.5 mm wide, prominently striate, deeply 5-lobed, the lobes triangular, acute, 2.5–3 mm long, to 3 mm wide.

In clearing and on plains, Costa Rica and Panama; closely related to *C. viride*.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 42* (F). Almirante region, Changuinola Valley, *Cooper III & Slater 34* (AAH, F, GH, US, YU).

8. **Citharexylum lankesteri** Moldenke, Feddes Repert. 37: 229. 1934.

Shrub or *tree* to 20 m tall; trunk to 60 cm diameter; branchlets stout, obtusely tetragonal, drying dark, densely stellate or tomentose with short whitish or grayish hairs, often leaf-scars borne on densely stellate ascending sterigmata to 11.5 mm long. *Leaves* opposite, entire, ovate-oblong or oblong-elliptic to obovate, 17–21 cm long, 7.3–8.3 cm wide, acuminate, subrevolute along the margins in drying, basally acute and slightly prolonged into the petiole, with a pair of elongate glands on the petiolar prolongation, firmly chartaceous, dark-green on both surfaces, shiny above, glabrous above except on the stellate midrib and secondary veins, beneath densely stellate-tomentose with many-branched hairs; minor venation abundant, conspicuous, mostly hidden by the pubescence beneath; petioles stout, margined, 2.3–3.5 cm long, drying dark, densely stellate-pubescent. *Racemes* axillary and terminal, erect or nutant, simple or the terminal one often with a basal pair of lateral branches, 10–27 cm long, loosely many-flowered; peduncles and rachis slender, densely stellate-tomentose, the peduncles 5–7.5 cm long; pedicels slender, to 2 mm long, stellate; foliaceous bracts and bractlets absent; prophylls linear-subulate, to 3 mm long, stellate; calyx campanulate-obconic, slightly curved and asymmetrical on the pedicel, ca. 3.6 mm long and 2.8 mm wide, 5-costate, puberulent, with 5 more or less recurved apicules; corolla hypocrateriform, the tube ca. 3.6 mm long, basally ca. 1.8 mm wide apically 2.8 mm wide, glabrous outside, densely tomentose in the throat, the lobes variable in size, broadly elliptic, mostly ca. 2.8 mm long and 2.6 mm wide, rounded, pubescent; fertile stamens subequal, not distinctly didynamous, inserted ca. 1 mm below the mouth of the corolla-tube and equaling it, the staminode filiform, ca. 1 mm long; style ca. 1.5 mm long, glabrous, the ovary obovate, conspicuously 2-lobed and 2-sulcate. *Fruit* subglobose, fleshy, slightly flattened laterally, bright yellow to russet red, to 2 cm in diameter, borne in pendent racemes, fruiting-calyx persistent.

Forested mountain slopes, ranging from El Salvador to Panama, mostly at high elevations.

CHIRIQUÍ: Slopes of Volcán Barú, near town of Cerro Punta, 6300 ft, *Stern & Chambers 98* (MO, MOLDENKE).

10. AEGIPHILA

Aegiphila Jacq., Obs. Bot. 2: 3. 1764.

Manabea Aubl., Hist. Pl. Guian. 1: 61. 1775.
Omphalococca Willd. *in* Roem. & Schult., Mant. 3: 10. 1827.
Amerina P. DC., Prodr. 9: 512–513. 1845.
Brueckea Klotzsch & Karst. *in* Karst., Ausw. Neu. Gew. Venez. 31. 1848.
Pseudaegiphila Rusby, Mem. New York Bot. Gard. 7: 339. 1927.

Woody plants, mostly *shrubs* or *trees*, sometimes scandent; branches and branchlets tetragonal or subterete, glabrous or variously pubescent. *Leaves*

simple, usually decussate-opposite, rarely subopposite or ternate, deciduous, exstipulate, mostly petiolate, glabrous or variously pubescent, entire or dentate. *Inflorescences* cymose, determinate, the cymes often paniculate, umbellate, capitate, reduced to few or solitary flowers, axillary or terminal. *Flowers* actinomorphic, hypogynous, hermaphroditic but usually conspicuously declinous; calyx gamosepalous, more or less campanulate, cyathiform or tubular, apically truncate and entire or 4- or 5-toothed or -lobed, accrescent, greatly incrassate and indurated in fruit; corolla gamopetalous, infundibular or hypocrateriform, mostly white or yellow, the tube cylindric, the limb equally 4- or 5-parted, the lobes imbricate in prefloration; stamens 4 or 5, equal, isomorphic, inserted below the mouth of the corolla-tube, included or exserted, alternate with the corolla-lobes, the filaments mostly filiform, the anthers often reduced but sometimes still polleniferous in pistillate flowers; pistil one, the style terminal or subterminal, single, capillary, mostly glabrous, the stigma bifid, its branches elongate and awl-shaped, the ovary superior, perfectly or imperfectly 4-celled, each cell 1-ovulate, the ovules lateral or sub-apical, hemianatropous. *Fruit* drupaceous, mostly fleshy, globose or subglobose, (1–3–)4-seeded, sometimes fewer by abortion; seeds without endosperm.

A complex genus of about 175 species and infraspecific taxa of subtropical and tropical America. *Aegiphila* ranges from Cuba and Mexico through the West Indies and Central America to Peru, and northern Argentina. One species is introduced in south Florida. Several species are sometimes cultivated as specimen plants. The Central American forms need further study, preferably in the field.

Aegiphila costaricensis Moldenke is a late addition to the treatment. It is described in Brittonia 1: 294. 1935, and in Fieldiana Bot. 24: 170. 1970. BOCAS DEL TORO: *Kirkbride & Duke 593* (MO); *Pittier & Tonduz 9167* (F, US); *Tonduz 8564* (US). DARIÉN: *Duke 6602* (MO).

a. Corolla-limb 5-parted; stamens 5 ..... 1. *A. anomala*
aa. Corolla-limb 4-parted; stamens 4.
  b. Inflorescence capitate, congested.
    c. Pubescence of branches, branchlets, and peduncles appressed, canescent ..... 2. *A. cephalophora*
    cc. Pubescence of branches, branchlets, and peduncles spreading, ferruginous ..... 16. *A. hoehnei* var. *spectabilis*
  bb. Inflorescence not capitate during anthesis, distinctly branched.
    d. Inflorescences axillary only.
      e. Leaf-blades distinctly serrate ..... 5. *A. odontophylla*
      ee. Leaf-blades entire.
        f. Branchlets glabrate, yellowish, shiny ..... 3. *A. laeta*
        ff. Branchlets densely canescent-pubescent ..... 4. *A. integrifolia*
    dd. Inflorescences either both axillary and terminal or only terminal and more or less thyrsoid.
      g. Calyx truncate or subtruncate during anthesis.
        h. Terminal panicles pendulous, long and narrow during anthesis ..... 6. *A. pendula*
      hh. Terminal panicles erect during anthesis.
        i. Branchlets glabrous.
          j. Leaf-blades conspicuously black-glandulose.
            k. Leaves manifestly falcate and conduplicate ..... 7. *A. glandulifera*
            kk. Leaves neither falcate nor conduplicate ..... 8. *A. panamensis*
          jj. Leaf-blades not conspicuously glandulose.
            l. Leaves large, broad, and falcate, 10–14 cm wide, broadly rounded at the base ..... 10. *A. falcata*
            ll. Leaves usually much narrower, not falcate, 3–10 cm wide ..... 9. *A. martinicensis*

ii. Branchlets not glabrous.
m. Branchlets, leaves, and inflorescences long-setose .. 14. *A. hirsutissima*
mm. Branchlets, leaves, and inflorescences not setose.
n. Branchlets densely pubescent ..... 13. *A. mollis*
nn. Branchlets merely puberulent.
o. Inflorescences few-flowered and lax; peduncles, pedicels, and sympodia more or less filiform and weak .... 12. *A. filipes*
oo. Inflorescences many-flowered; peduncles, pedicels, and sympodia firm.
p. Fruiting-calyx subtruncate and entire.
q. Leaf-blades conspicuously marked beneath with large black glandular disks; fruiting-calyx cupuliform, closely investing the fruit ..... 8. *A. panamensis*
qq. Leaf-blades not glandular; fruiting-calyx shallow, not closely investing the fruit ..... 11. *A. magnifica*
pp. Fruiting-calyx deeply lobed or split.
r. Leaf-blades mostly glabrous on both surfaces, without glandular disks beneath ..... 9. *A. martinicensis*
rr. Leaf-blades densely puberulent on both surfaces, with black glandular disks beneath ..... 11a. *A. magnifica* var. *pubescens*
gg. Calyx distinctly toothed, lobed, or split during anthesis.
s. Leaf-blades glabrous or glabrate beneath ..... 15. *A. elata*
ss. Leaf-blades densely hairy beneath.
t. Cymes congested, densely hirsute, bracteoles conspicuous ..... 16. *A. hoehnei* var. *spectabilis*
tt. Cymes open, densely short-pubescent; bracteoles not conspicuous .... 17. *A. deppeana*

1. **Aegiphila anomala** Pittier, Contr. U. S. Natl. Herb. 12: 191, *fig. 19*. 1909.

Small *tree* to 15 m tall, of sparsely branched, open spreading growth; trunk to 1 m in diameter at base; bark brown, thick, cork-like, sutured, much roughened and shaggy by raised and slightly curled granulated narrow-oblong strips; branchlets stout, grayish, acutely tetragonal, manifestly decussate-ampliate and flattened upwards, roughened-puberulent; leaf-buds round, gray-green; leaf-scars elevated, vertically elongate, narrow, ca. 3 mm long and 2 mm wide, the edges not at all sharp or prominent. *Leaves* large, opposite, bunched at the ends of the branchlets; coriaceous, lanceolate or obovate, 7–24 cm long, 6–7 cm wide, obtusely acuminate, entire or slightly revolute-margined, basally long-cuneiform and attenuate into the petiole, petioles stout, 1–2 cm long, puberulent; dark and shiny above, paler beneath, minutely puberulent on both surfaces, probably glabrate in age, secondary veins 12–16 pairs, arcuate-ascending, obscure above, prominent and densely puberulent beneath, plainly anastomosing along the margins beneath; minor venation sparse, inconspicuous. *Inflorescences* axillary, solitary, opposite, cymes to 3 cm long, brachiate, few-flowered, loose; peduncles ca. 5 mm long, stout, puberulent, verrucose; pedicels slender, ca. 5 mm long, incanous-pubescent, thickened and verrucose in fruit; bractlets and prophylls minute, subulate, pubescent. *Flowers* with buds buffy-yellow or grayish-yellow; the flowers very odorous; calyx narrowly campanulate, 10–11 mm long, ca. 6 mm wide, pubescent, the rim 3–5 parted, the lobes irregular, ca. 3 mm long, slightly emarginate; corolla white, rotate or hypocrateriform, 14–20 mm wide when fully expanded, the tube conconic or urceolate, 4.5–7 mm long, included in the calyx, the lobes 5, broadly ovate-lingulate, 6–6.5 mm long, ca. 3.7 mm wide, obtuse, sometimes recurved; stamens 5, equal, inserted

ca. 2.5 mm below the mouth of the corolla-tube, scarcely exserted in pistillate flowers and long-exserted and curvate in staminate flowers, the filaments fine pubescent; pistil exserted in pistillate flowers, the style ca. 5 mm long, shorter in staminate flowers, glabrous, the stigma-branches filiform, ca. 3.7 mm long, papillose, the ovary spherical, dark, ca. 0.6 mm long and wide, glabrous, 4-celled. *Fruit* hard, light-colored, oblong, ca. 9 mm long and 8 mm wide, conspicuously flattened and umbilicate at the apex, 4-seeded; seeds large, nut-like, furrowed; fruiting-calyx greatly enlarged and indurated, verruculose, gray, obvolute and cucullate, somewhat irregularly lobed or splitting, ca. 15 mm long and 12 mm wide, glabrate, completely enclosing the fruit.

In open forests and on wooded hillsides, Costa Rica and Panama; closely related to *A. valerii* Standl. of Costa Rica.

"Tabaquilla."

CANAL ZONE: Barro Colorado Island, *Croat 4326, 6629* (both NY). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2350* (MO).

2. **Aegiphila cephalophora** Standl., Publ. Field Columbian Mus. Bot. Ser. 4: 156. 1929.

Vine, often high-climbing; branchlets slender, tetragonal, densely appressed-pubescent with long white antrorse hairs; leaf-scars projecting conspicuously; buds woolly. *Leaves* opposite, subcoriaceous, entire, ovate or ovate-oblong, 9–13.5 cm long and 4.5–7.5 cm wide, abruptly rounded to an acuminate point ca. 1 cm long, basally subacute or rounded, dark and shiny above, lighter and densely tomentose beneath, more sparsely so above, especially along the midrib; midrib prominent and pubescent on both surfaces; secondary veins in ca. 7 irregularly placed pairs, anastomosing near the margins; petioles stout, 5–7 mm long, densely long pubescent. *Inflorescences*, axillary and terminal, cymes, opposite, capitate, dense-flowered, the uppermost pair usually short pedunculate and much like a single terminal one; peduncles densely long-pubescent, the upper ones ca. 5 mm long, the lower ones 1.5–2.5 cm long; pedicels, bractlets and prophylls hidden by the long matted white pubescence. *Flowers* with the calyx thin, obconic, ca. 2.5 mm long and wide, densely pubescent outside with white hairs 2.3–2.6 mm long, glabrous within, apically 4-mucronulate or subentire; corolla white, infundibular, the tube ca. 3.1 mm long, glabrous or slightly granular-pulverulent, the lobes (3–)4, broadly ovate- or elliptic-lingulate, acute, ca. 3.1 mm long and 2.3 mm wide, glabrous; stamens 4 inserted just beneath the mouth of the corolla-tube, long-exserted in staminate flowers, the filaments ca. 4.7 mm long, glabrate; pistil equaling the corolla or slightly exserted in staminate flowers, the style ca. 2.1 mm long, glabrous, stigma-branches ca. 2 mm long, the ovary depressed-globose, ca. 0.5 mm long and wide, glabrous, 4-lobed, 4-celled. *Fruit* orange, 1.5 cm diameter; fruiting clusters pendent.

Occurring at forest edges, this species is endemic to Panama. The plant has been described as a tree, perhaps in error.

The densely appressed-pubescent branchlets with long white antrorse hairs distinguish this species from the otherwise similar *Aegiphila deppeana*, where the pubescence spreads at right angles to the branchlets and is more buff-colored.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 662* (BH, F). Barro Colorado Island, near Armour House, *Bangham 543x* (AAH, F). Forest margin, road to Battery VII NW part of Canal Zone, *Johnston 1661* (MO). Barro Colorado Island, *Kenoyer 607* (F). Barro Colorado Island, Miller Point, *Shattuck 988* (MO). Without locality, *Aviles 988* (F).

3. **Aegiphila laeta** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 202. 1817.

A. stricta Rusby, Descr. 300 New Sp. S. Amer. Pl. 107. 1920.

Shrub or low *tree*, 2–12 m tall, sometimes appearing herbaceous when young; branches stout, strict, acutely tetragonal, greatly flattened and ampliate at the nodes, sulcate along the sides, shiny, minutely puberulent or glabrate; branchlets slender, obscurely or obtusely tetragonal, shallowly sulcate along the sides, decussately ampliate at the nodes, yellowish, shiny, subglabrate. *Leaves* opposite; thin-membranous or chartaceous, usually fragile when dry, oval or somewhat obovate, 5–10 cm long, 2–4 cm wide, apically abruptly contracted and long-acuminate or sometimes rounded and bluntly acute, entire, basally abruptly and shortly produced into the petiole, light-green shiny and glabrate on both surfaces; secondary veins slender, 7–10 pairs, strongly arcuate-ascending, slightly prominulent beneath, minor veins delicate and inconspicuous; petioles slender, weak, 8–12 mm long, basally annulate, minutely puberulent. *Inflorescences* axillary, solitary, opposite, cymes ca. ⅓ as long as the subtending leaves, 2–4 cm wide, trichotomous, loose and spreading, bracteate, laxly many-flowered; peduncles slender, 1.5–3 cm long, minutely puberulent or cinereous; pedicels slender, ca. 2 mm long, minutely puberulent; bractlets and prophylls subulate, 1–2 mm long, puberulent. *Flowers* faintly fragrant; calyx light-green and membranous, campanulate or turbinate, ca. 2.5 mm long and 2 mm wide, glabrate, lax around the corolla-tube, shallowly 4-lobed, the lobes erect, broadly ovate, rounded; corolla pale-yellow, cream-color, or yellowish-white to white, infundibular, the tube narrowly cylindric, 5–8 mm long, the lobes 4, erect, broadly ovate-lingulate, rounded; ca. 3 mm long and 2.6 mm wide, stamens 4, inserted ca. 1 mm below the mouth of the corolla-tube, included in pistillate or long-exserted in staminate flowers, the filaments 2–7 mm long, glabrous; pistil included in staminate flowers, the style ca. 2 mm long, glabrous, the stigma branches 1–3 mm long, ovary rotund, ca. 0.2 mm long and wide, yellowish, glabrous; fruit ca. 5 mm long and 6 mm wide, orange or red, distinctly 4-lobed, roughened and drying black, very shallowly invested by the fruiting-calyx; seeds 3 or 4.

Low forest, thickets, and clearings, mostly at low altitudes, often near the seashore, Panama to Venezuela.

"Manprasara" and "San Juan de verdad."

CANAL ZONE: Beyond Madden Dam bridge, *Correa & Dressler 351* (MO). Near Miraflores Lake, *White 175* (NY). DARIÉN: Near Santa Fé, Río Sabana, *Duke 4116* (MO, MOLDENKE). Quebrada Nigua below Santa Fé, *Duke 8827* (BMIC, MO). PANAMÁ: Bushy shaded ravines, Taboga Island, *Barclay 2498* (BM, NY). Logging roads, Río Pita, 1–3 mi. above Río Maestra, *Duke 4762* (MO). Thicket, Bald Hill Road, San José Island, *Johnston 56* (MO, US). SAN BLAS: Above Ailigandi River, *Duke & Bristan 348* (AAU). Nakka Island, *Dwyer 6871* (MO).

4. **Aegiphila integrifolia** (Jacq.) Jacq. *ex* Jacks., Ind. Kew. 1: 46. 1893.

Callicarpa integrifolia Jacq., Enum. Syst. Pl. 12. 1760.
Manabea arborescens Aubl., Hist. Pl. Guian. 1: 64. 1775.
Aegiphila arborescens (Aubl.) J. F. Gmel. *in* L., Syst. Nat., ed. 13. 2: 259. 1789.
Callicarpa globiflora Ruiz & Pav., Fl. Peruv. 1: 49, *pl. 77b*. 1798.

Shrub or slender *tree* 3–12 m tall; trunk to 30 cm in diameter, straight; wood light-colored, thin and the pith ample; outer bark gray, rough; inner bark thick, clear-chestnut or dark-red; branches and branchlets acutely tetragonal, deeply canaliculate along the sides, decussately flattened and ampliate at the nodes, densely incanous-pubescent or sericeous. *Leaves* slightly aromatic, opposite or rarely approximate, membranous or chartaceous, oblong to elliptic or obovate, 7.5–35 cm long and 3.5–15 cm wide, acuminate, entire or denticulate, basally long-attenuate and decurrent into the petiole, shiny-green above, paler beneath, appressed hirtellous with incanous hairs above, glabrescent but slightly roughened in age, beneath appressed sericeous-puberulent with incanous hairs, especially along the midrib and larger veins and dotted with cutaneous glands, petioles 4–13 mm long, incanous-pubescent; minor veins slender and delicate. *Inflorescences* axillary, solitary, opposite, cymes to half as long as the subtending leaves, di- or trichotomous, globose or capitate-corymbose when young, densely many-flowered but becoming somewhat more loosely flowered, bracteolate; flowers manifestly declinous; peduncles slender, 2–5 cm long, shorter in the pistillate flowers than in the staminate, flowers often flattened and distinctly canaliculate, densely strigose-sericeous and incanous; pedicels filiform, to 5 mm long in the staminate flowers, short or obsolete in the pistillate, incanous-pubescent; bractlets and prophylls usually absent, or when present, few, linear, subulate, firm, short and incanous. *Flowers* copious, calyx clavate-infundibular, subturbinate-tubular, in the pistillate more usually tubular-campanulate, subangular, firmly membranous or subherbaceous, 5–8 mm long, 3 mm wide, densely incano-sericeous outside, softly sericeous within, lax around the corolla-tube, acutely 4-dentate, 4-lobed, or 4-parted, the segments ovate, acute, often spreading; corolla infundibular, white or yellowish, the tube cylindrical, slender, 4–12 mm long, puberulent upwards, the lobes 4, ovate- or lanceolate-lingulate, acute, 2–4 mm long, ca. 2 mm wide, spreading, often reflexed, stamens 4, inserted ca. 1 mm below the mouth of the corolla-tube, exserted in the staminate flowers or equaling the corolla-tube in the pistillate, the filaments 0.2–7 mm long, glabrous; pistil included in the staminate flowers or exserted in the pistillate, the style 3.7–7 mm long, glabrous, the stigma branches 2.4–3.4 mm long, longer in the pistillate, flowers papillose, ovary subglobose, ca. 1 mm long and wide, flat at both ends, glabrous, apically 4-lobed, 4-celled. *Fruit* borne in heavy clusters, subglobose or obovate, ca. 8 mm long and 7 mm wide, apically depressed, smooth and shiny, green or yellow, becoming orange, 2–4 seeded, the base invested by the fruiting-calyx; seeds ovate, plano-convex, with a subcrustaceous testa; fruiting-calyx greatly enlarged and indurated, cupuliform, shallowly and irregularly lobed, enclosing the base of the fruit.

Occurring in woods and thickets, along the banks of streams, on abandoned land, at the edge of clearings, and on savannas, this species is widely distributed from Trinidad and Panama to southern Brazil, Bolivia and Peru.

"Carindiba," "lardwood," and "tocaneiro."

DARIÉN: Near Cana, 1750 ft, *Stern et al. 663* (MO).

5. **Aegiphila odontophylla** Donn. Sm., Bot. Gaz. (Crawfordsville) 25: 157. 1898.

A. aculeifera Moldenke, Feddes Repert. 37: 209. 1934.

Shrub or *tree*, to 10 m tall; branches and branchlets stout or slender, obtusely tetragonal, flattened and ampliate at the nodes, densely and irregularly granulose- or furfuraceous-tomentellous with pale ochraceous hairs, more or less verruculose with numerous elevated lenticels and armed with short and more or less recurved prickles. *Leaves* opposite; thin-membranous, oblong-obovate or obovate-elliptic, often undulate in drying, 7–21 cm long, 2.7–9.5 cm wide, abruptly acute or short-acuminate, regularly serrulate with glandulose-mucronate-antrorse teeth, basally acute to cuneate and somewhat attenuate into the petiole, deep-green and shiny above, somewhat lighter beneath, granulose-tomentellous or furfuraceous-pubescent on both surfaces, especially along the venation, glabrescent except on the veins, petioles 0.6–3.2 cm long, furfuraceous or ochraceous-tomentellous; *Inflorescences* axillary or supra-axillary, solitary, opposite, cymes 2–4.5 cm long, 3–6 cm wide, much shorter than the subtending leaves, usually manifestly bifurcate, often copiously armed with small recurved prickles, loosely many-flowered, bracteolate, often reduced upwards, peduncles 0.8–1.7 cm long, furfuraceous, often copiously prickly; pedicels furfuraceous, 1–3 mm long in the uppermost cymes, 3–10 mm long in the lower and larger cymes; calyx obconic or obconic-campanulate, 5–7 mm long 4–5.3 mm wide, more or less densely furfuraceous, verruculose, often with a few large glands outside, 2- or 4-lobed, the lobes equal, 1.5–2.1 mm long, semiorbicular, truncate, apiculate with an excurrent vein; corolla hypocrateriform, white or pinkish-white, the tube cylindric, 8–8.3 mm long, glabrous outside, pubescent within, the lobes 4, oval- or oblong-lingulate, 5–6.3 mm long, 3.1–3.2 mm wide, subacute or obtuse; stamens 4, inserted ca. 3.6 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers, the filaments flattened, 2.1–10.8 mm long, pilose toward the base; pistil glabrous, included in the staminate flowers, the style 5.2–6.4 mm long, the stigma branches 2.1–3.9 mm long, the ovary ovate or pyriform, subtetragonal, truncate at both ends, ca. 1 mm long and wide, obscurely 4-lobed, 4-celled. *Fruit* pale-yellow and semi-pellucid.

In forests and in semi-shade at edges of forest at higher altitudes from Costa Rica to Colombia and Venezuela.

"Tabaquilla."

BOCAS DEL TORO: Between Quebrada Gutierrez and the east slope of La Zorra, headwaters of Río Mali, *Kirkbride & Duke 714* (MO). Secondary growth, Gutierrez, Chiriquicito-Caldera Trail, *Kirkbride & Duke 753* (MO).

6. **Aegiphila pendula** Moldenke, Feddes Repert. 33: 135. 1933.

Scandent or scrambling *shrub* ca. 2–6 m tall, branches and branchlets slender, arching, obtusely tetragonal, densely puberulent throughout. *Leaves* opposite or (on young shoots) approximate; chartaceous, entire, oblong, 10–24 cm long, 3.5–10 cm wide, acuminate, basally acute or acuminate, dark-green above, paler

beneath, sparsely and minutely strigillose with short white antrorse hairs on both surfaces, glabrescent, secondary veins 10–12 pairs, minor venation delicate and inconspicuous, petioles slender, very weak, 7–14 mm long, puberulent or glabrate. *Inflorescences* axillary cymes and terminal panicles; the cymes solitary, opposite, ca. 5 cm long and 3 cm wide, many-flowered, dense, bracteolate; the panicles narrow throughout, 25–50 cm long, 10–12 cm wide, pendent or nutant during anthesis and fruit, foliose, the component cymes ca. 8 cm apart below, the internals gradually decreasing upwards, the sympodia slender, conspicuously sulcate, puberulent; peduncles slender, 1.5–5 cm long, tetragonal and sulcate, puberulent; pedicels slender, 4–6 mm long, puberulent; bracts numerous, large, foliaceous, oblong, similar to the leaves but smaller, to 11 cm long and 4.5 cm wide; bractlets lanceolate or linear, 5–10 mm long; prophylls minute, subulate; *flowers* with the calyx campanulate, shallow and lax, ca. 2 mm long and 3 mm wide, puberulent, subtruncate, 4-apiculate; corolla white or pale-yellow, infundibular, the tube narrow-cylindric, ca. 4.3 mm long, abruptly ampliate above, the lobes 4, oblong-lingulate, ca. 3.7 mm long and 2.5 mm wide, rounded; stamens 4, inserted ca. 0.3 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers, the filaments ca. 8 mm long, glabrous; pistil included in the staminate flowers, the style ca. 1.6 mm long, glabrous, the stigma branches ca. 1 mm long, the ovary subrotund, ca. 1 mm long and wide, apically 4-lobed, glabrous, 4-celled. *Fruit* depressed-globose, yellow, ripening orange, to 5 mm long and wide, glabrous, basally invested for about 1.5 mm by the closely fitting fruiting-calyx; fruiting-calyx greatly enlarged and indurated, cupuliform, ca. 2 mm long and 5 mm wide, abruptly narrowed into the ampliate fruiting-pedicel, puberulent, closely investing the fruit, apically truncate and entire.

In forests and at the edges of swamps from Panama to Venezuela and Ecuador.

CANAL ZONE: Road to Tortuguilla Point, NW part of Canal Zone, *Johnston 1606* (MO). Edge of mangrove swamp, just south of Fort Sherman, *Johnston 1683* (MO). Wet forest, Las Cascadas Plantation near Summit, *Standley 25719* (US).

7. **Aegiphila glandulifera** Moldenke, Brittonia 1: 187. 1932.

Bushy *shrub*, *tree*, or *vine* to 20 m tall, with sickening fetid odor; trunk to 60 cm d.b.h.; branches and branchlets stout, obtusely tetragonal or subterete, brown, glabrate; leaf-scars often prominent. *Leaves* opposite, chartaceous, entire, oblong, 12–22 cm long, 4.5–10 cm wide, mostly more or less falcate and conduplicate, acute or acuminate, basally acute or acuminate at the base, green above, lighter beneath, glabrate but densely punctulate on both surfaces, usually marked with numerous black glandular disks along the midrib beneath, secondary veins 10–16 pairs, anastomosing near the margins; petioles dark, 9–13 mm long, glabrous. *Inflorescences* axillary cymes and terminal panicles; the cymes solitary, opposite, to 9 cm long and 6 cm wide, often abbreviated, brachiate, many-flowered, bracteolate; the panicles thyrsoid, to 23 cm long and 13 cm wide, sometimes narrow and abbreviated or greatly elongated, often very dense and congested, bracteate, the sympodia stout, sulcate, glabrous, often composed of 19 or more cymes, peduncles to 3 cm long, glabrous; pedicels ca. 2 mm long glabrate or puberulent; bracts large and foliaceous, numerous in the terminal panicle; bract-

lets linear; prophylls subulate. *Flowers* with the calyx cupuliform or campanulate, ca. 1.8 mm long and 2.6 mm wide, glabrate, lax around the corolla-tube, subtruncate, entire or 4-apiculate; corolla greenish-yellow or light-yellow to cream-colored or white, sometimes light-lilac, hypocrateriform, long-persistent, the tube narrow-cylindric, ca. 7.8 mm long, glabrous, the lobes 4, oblong-lingulate, ca. 4.6 mm long and 2.3 mm wide, acute; stamens 4, inserted ca. 1.3 mm below the mouth of the corolla-tube, exserted in the staminate flowers or included in pistillate, the filaments 1–12.4 mm long, glabrous; pistil long-exserted in the pistillate flowers or included in staminate, the style 3.6–9.3 mm long, glabrous, the stigma branches ca. 4.6 mm long, the ovary subglobose, ca. 1 mm long and wide, glabrous, 4-celled. *Fruit* ochraceous, later black, oblong-elliptic, 8–10 mm long, 6–9 mm wide, glabrous; fruiting-calyx cupuliform, 4–4.5 mm long, ca. 9 mm wide, minutely pulverulent-puberulent, truncate, entire or slightly erose.

In forests and clearings from Costa Rica to Amazonian Peru and Brazil.

"Chirapa sacha."

BOCAS DEL TORO: Little Bocas, near Chiriqui Lagoon, *von Wedel 2517* (MO, US). CANAL ZONE: Gatun Station on Panama Railroad, *Hayes 74* (GH), *253* (NY). Gatun, *Hayes 145* (NY). Empire Station, *Hayes 269* (BM, K), *Hayes s.n.* (E). Around Gamboa, *Pittier 6519* (GH, K, US). Panama, *Seemann* 335 (BM). Old Fort San Lorenzo, *Tyson 2213* (MO). Near Miraflores Lake, *White 255* (NY).

8. **Aegiphila panamensis** Moldenke, Trop. Woods 25: 14. 1931.—FIG. 10.

A. paniculata Moldenke, Trop. Woods 25: 16. 1931.

Shrub or small *tree* to 10 m tall or *vine-like*; trunk straight, erect, cylindric; bark grayish-white, minutely scored vertically with shallow confluent furrows and scaling off in small plates between the furrows; branches ascending, irregularly opposite, almost white; wood creamy-white, with a somewhat aromatic odor; branchlets slender or rather stout, elongate, obtusely tetragonal or subterete, flattened and ampliate at the nodes, usually conspicuously flattened and sulcate toward the tips, gray-green or brownish, densely puberulent, rarely glabrate, often becoming furrowed in drying. *Leaves* opposite, membranous or chartaceous, entire, lanceolate or oblong to oblong-lanceolate or obovate, 9–18 cm long, 3–8 cm wide, acute to long-acuminate or caudate, basally acute or acuminate and sometimes narrowly attenuate into the petiole, dark-green above, paler beneath, blackening in drying, densely roughened-puberulent on both surfaces, especially along the midrib and secondary veins, probably glabrescent, densely and minutely glandular-punctate beneath, usually with numerous glandular disks of varying dimensions scattered on the lamina along both sides of the midrib beneath, disappearing upwards, secondary veins 8–12 pairs, mostly prominent on both surfaces, minor veins slender and delicate but usually conspicuous beneath; petioles slender or stoutish, weak, 5–13 mm long, spreading, puberulent or glabrate. *Inflorescences* axillary cymes and terminal panicles; the cymes solitary, opposite, to 10 cm long and 6.5 cm wide, half as long as the subtending leaves or less, often densely many-flowered, bracetolate, the panicles pyramidal, usually large and thyrsoid, sometimes long and narrow, to 30 cm long, basally to 21 cm wide, the branches ca. 5 pairs or numerous, opposite or approximate, 2–3 cm long,

FIGURE 10. *Aegiphila panamensis* Moldenke—A. Habit (× 5/9). [After *Woodson et al.* 1756 (MO).]—B. Flower (× 4½). [After *Allen* 856 (MO).]

usually trifurcate, many-flowered, bracteate, the sympodia variable in length, often elongate, stout, 2–5 cm long, usually conspicuously flattened and sulcate, brownish, furrowed in drying, densely puberulent or glabrate; peduncles 1–6 cm long, terete, furrowed in drying, brownish, usually puberulent, sometimes glabrate; pedicels slender, 1–2 mm long, puberulent, the lateral ones 1–2 mm long, the central ones shorter or obsolete, puberulent; bracts large and foliaceous, similar

to the leaves but smaller, mostly lanceolate, 6–10 cm long and 1–2 cm wide, acuminate at both ends, densely puberulent on both surfaces and with many glandular disks along the midrib; bractlets linear or narrow-lanceolate, to 16 mm long and 7 mm wide, caducous; prophylls linear, 1–5 mm long, caducous. *Flowers* with the calyx obconic-campanulate, ca. 2.8 mm long and 2.3 mm wide, puberulent, truncate or minutely 4-apiculate; corolla hypocrateriform, pale- or lemon-yellow to white, the tube narrow-cylindric, 5–7.5 mm long, ampliate above, glabrous outside, pubescent within, the lobes 4, oblong-lingulate, ca. 4.1 mm long and 2.3 mm wide, obtuse; stamens 4, inserted ca. 2.8 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers or included in the pistillate, the filaments flattened, 0.7–10.4 mm long, somewhat pilose; pistil included or equaling the corolla-tube in the staminate flowers, long-exserted in the pistillate, the style 5.2–12 mm long, glabrate, the stigma branches 0.5–2.6 mm long, the ovary dark, oblong, ca. 1 mm long and 0.5 mm wide, apically flattened and umbilicate, glabrous, 4-lobed, 4-celled. *Fruit* yellow or orange, oblong, tetragonal, 9–10 mm long and ca. 7 mm wide, flattened and conspicuously umbilicate apically, smooth and shiny, drying brown, smooth and shiny, gibbous at the middle, 4-seeded; seeds white; fruiting-calyx large and indurated, cupuliform, usually very distinctly tetragonal, basally flat and truncate, 2–5 mm long and 7–10 mm wide, externally puberulent, glabrous and shiny within, its rim usually very regular and truncate, fitting closely over the base of the mature fruit like the cup of an acorn or subincluding the very immature fruit, the pedicels greatly incrassate and acutely tetragonal in fruit, ampliate to ca. 1.2 mm above.

In forests and thickets, from southern Mexico to northern Colombia.

A variable species, closely related to the West Indian *A. martinicensis*.

BOCAS DEL TORO: Changuinola, *Stork 20* (MICH, US), *Stork 48 1/2* (F, US). Changuinola Valley, *Cooper & Slater 40* (F, US, YU), *117* (GH, NY, US, YU); Changuinola, *Dunlap 20* (F), *407*, *Dunlap 438* (both F, US). Near Chiriquí Lagoon, *von Wedel 1221* (MO, NY). CANAL ZONE: Near Summit, *Standley 25808* (US). Near Culebra, *Standley 25956* (US). Sosa Hill, *Standley 26465* (AAH, S, US). Near Fort Kobbe, *Allen 2016* (MO, NY). Near Fort Sherman, *Blum & Dwyer 2103* (MO). West end of Gatun Lake dam, *Blum & Tyson 1993* (MO). Beyond Madden Dam bridge 1 mi, *Correa & Dressler 351* (NY). Barro Colorado Island, *Croat 4094* (LL), *6580* (AAU), *6749* (AAU), *7089* (AAU). Casa Larga Trail, forest along telephone trail between Río Indio Hydrographic Station and the Natural Bridge of Río Puente, *Allen 17471* (MICH, MO). Farfan Beach, *Dwyer 2873* (MO). Fort Sherman, *Dwyer 7172* (MO, US). Between Summit and Gamboa, *Greenman & Greenman 5227* (MO). Between Frijoles and Monte Lirio, *Killip 12171* (NY, PH, US). Disturbed forest, near Madden Dam 50 ft, *Lewis et al. 20* (MO). Barro Colorado Island, *Moldenke & Moldenke 19896* (LEMPERG, NY). Brushy slope along the Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29232* (US). Fort Sherman on Pena Road, *Tyson & Chu 1713* (MO). Near Miraflores Lake, *White 255* (MO). COCLÉ: Advanced secondary rainforest, Boca del Toabre at Río Toabre and Río Cocle del Norte, *Lewis et al. 1247*, *1249*, *1756* (all MO, NY). COLÓN: Río Culebra above Santa Isabel near sea level, *Pittier 4149* (GH, NY, US). Wooded swamp between France Field, *Standley 30246* (US). DARIÉN: Near Yape, ca. 30 m, *Allen 856* (MO). Near Boca de Cupe, ca. 40 m, *Allen 906* (MO, NY). 1–3 mi. SW of Santa Fé on the PanAm Highway, *Duke 4095* (MO, UC). 1–3 mi. SE of Santa Fé on the PanAm Highway, *Duke 4109* (MO, MOLDENKE). PANAMÁ: Shrubby or forested ravines in the "savanna" zone, Cerro Campana, *Bartlett & Lasser 16901* (MICH). Near Pacora, ca. 35 m, *Allen 1123* (F, MO). Near La Jagua, *Bartlett & Lasser 16998* (MICH). Panamá, *Duchassaing*, 1851 (P); *Bro. Paul 158* (US); *Seemann s.n.* (K); *Standley 26684*, *30496* (both US). Ca. 1 mi. E of Tocumen Airport on side road off of Inter-American Highway, *Blum & Tyson 1955* (MO). Near El Llano, *Duke 5514*, *5866* (both MO). Panamá, *Hayes*, 1962 (NH). Camino de la Granja,

Bro. Heriberto 163 (NY, US). Sabana de Juan Corso near Chepo, 60–80 *m*, *Pittier 4501* (NY, US). Agricultural Experiment Station at Matías Hernández, *Pittier 6815* (NY, US). In thicket, *Bro. Heriberto 163* (NY, US). Sabana de Juan Corso near Chepo, 60–80 m, *Pittier 4501* (NY, US). SAN BLAS: Near Mandinga on San Blas mainland, *Duke 8889* (BMIC). Mainland point opposite Isla Mosquito, *Duke 8983* (MOLDENKE). Marshy rainforest, mainland opposite Ailigandi, *Lewis et al. 157* (MO), *201* (MO, NY).

9. **Aegiphila martinicensis** Jacq., Obs. Bot. 2: 3, *pl. 27*. 1764.

A. dumosa Salisb., Prodr. 67. 1798.
A. diffusa Andr., Bot. Repos. 9: 578. 1809.
A. glabra Poir., Encycl. Méth. Suppl. 1: 150. 1810.
A. straminea Hoffmgg., Verz. Pfl. Nachtr. 3: 18. 1826.
A. macrophylla Desf., Cat. Pl. Hort. Reg. Paris., ed. 3. 391. 1829, non *A. macrophylla* H. B. K., Nov. Gen. Sp. Pl., ed. folio. 2: 204. 1817.
Psychotria corymbosa Sieber *in* DC., Prodr. 4: 523. 1830.
Aegiphila magnifolia Steud., Nom. Bot., ed. 2. 1: 29. 1840.
A. grandifolia Walp., Repert. Bot. Syst. 4: 121. 1845.

Shrub or slender *tree* 1–5 m tall; branches obtusely tetragonal or subterete, minutely puberulent, glabrescent; branchlets obtusely tetragonal, ampliate and compressed at the nodes, softly puberulent or glabrescent; bark light-gray; leaf-scars borne on oblique sterigmata. *Leaves* opposite, spreading, variable, usually membranous, sometimes chartaceous, entire, oblong-lanceolate to oblong, 8–25 cm long, 3–10 cm wide, acuminate or coarctate-attenuate into a narrow and abrupt point, basally narrowed and acute to obtuse or rounded, bright-green and shiny above, pale beneath, usually glabrous and smooth on both surfaces, sometimes faintly puberulent or glandular-punctate; petioles slender, weak, 5–14 mm long, minutely puberulent. *Inflorescences* axillary cymes and terminal panicles; the cymes solitary, opposite, corymbose or sometimes subcomposite, spreading, many-flowered, more or less trichotomous, half as long or equaling the subtending leaves, often diminishing upwards; the panicles thyrsoid, often pyramidal, to 17 cm long and 13 cm wide, leafy, the sympodia fastigiate, stout, puberulent or glabrate; peduncles 2.5–7.5 cm long, puberulent; pedicels 2–4 mm long, minutely puberulent, often 2-bracteolate below the middle, not much thickened in fruit; bractlets and prophylls linear or subulate, 1–2 mm long, puberulent. *Flowers* inodorous; the calyx narrow-campanulate or turbinate-infundibular, widening from an acute base to a cupuliform limb, 2–3 mm long and 1.5–3 mm wide, lax around the corolla-tube, minutely puberulent or glabrous, truncate, subentire or 4-mucronulate; corolla white or pale-yellow, hypocrateriform, the tube narrow-cylindric, 2–6 mm long, ampliate above, the lobes usually 4, ovate-lingulate, 2.3–6.5 mm long and 1.7–3.7 mm wide, obtuse, often minutely puberulent outside; stamens usually 4, inserted 1–3 mm below the mouth of the corolla-tube, exserted in the staminate flowers or included in the pistillate, the filaments 0.6–7.2 mm long, glabrous; pistil included in the staminate flowers or exserted in the pistillate, the style 3–9 mm long, glabrous, the stigma branches 1–4 mm long, often widely divergent in the pistillate flowers, the ovary subglobose, 1–1.5 mm long and wide, flattened above, 4-sulcate, glabrous, 4-celled. *Fruit* subglobose or ovoid, 5–13 mm long and 8–10 mm wide, yellow or red, umbilicate at both ends with little soft pulp, blackening and becoming deeply 4-lobed and roughened in drying, hardly invested at the base by the fruiting-calyx, 4-seeded; fruiting-calyx greatly enlarged

and indurated, shallowly cupuliform or patelliform, lax and spreading, ca. 6 mm wide, irregularly lobed with large rounded lobes, often veiny, scarious-margined.

In forest, thickets, and the margins of woods throughout the West Indies to Trinidad, Panama, Colombia, and Venezuela.

"Wild-jasmine," "goatwood" (English), "capaillo," "lengua de vaca" (Spanish), etc.

The following collections are assigned to this species with hesitation: they need further study.

BOCAS DEL TORO: Region of Almirante, *Cooper 571* (F, K, NY, S, US, YU). CANAL ZONE: Low wooded inland area, Fort Kobbe, *Duke 4685* (UC).

10. **Aegiphila falcata** Donn. Sm., Bot. Gaz. (Crawfordsville) 18: 7, as "*Aegyphila.*" 1893.

Shrub or symmetrical *tree* 5–13 m tall or scandent; branchlets stout, acutely tetragonal, flattened and ampliate at the nodes, the sides deeply canaliculate, glabrous or minutely puberulent. *Leaves* opposite, large, spreading; membranous, extremely brittle in drying, entire, oval or obovate-oblong, variable in size but usually very large, 17–38 cm long and 10–14 cm wide, broadly rounded or abruptly short-acuminate, basally broadly rounded, usually more or less falcate and conduplicate, especially at the base, light-green and shiny, glabrous and faintly glandular-punctate or minutely puberulent on both surfaces; petioles stout, 12–18 mm long, glabrous or minutely puberulent. *Inflorescences* terminal thyrsoid panicles to 18 cm long and 13 cm wide or bracteate, the sympodia fastigiate, acutely tetragonal and canaliculate, complanate at the nodes, glabrate or finely puberulent throughout; cymes axillary, long-pedunculate, less than half as long as the subtending leaves; peduncles 1.5–3 cm or more long, glabrate or minutely puberulent; pedicels ca. 3 mm long, puberulent; bracts foliaceous, lanceolate, often absent; bractlets and prophylls subulate, 1–2 mm long. *Flowers* abundant, calyx obpyramidal, ca. 3.5 mm long and wide, finely puberulent, subtruncate or with irregular and shallowly repand lobes; corolla white, greenish-yellow, to orange, hypocrateriform, the tube narrow, 3–15 mm long, gradually ampliate above, the 4-lobes oblong-lanceolate, ca. 6.2 mm long and 2 mm wide, subacute; stamens 4, inserted ca. 1.3 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers or included in the pistillate, the filaments 3.5–10 mm long, glabrous; pistil included in the staminate flowers or long-exserted in the pistillate, the style 3.2–8.5 mm long, the stigma branches ca. 2.5 mm long, the ovary subrotund, light, ca. 1.1 mm long and wide, glabrous, flattened and 4-lobed above, 4-celled. *Fruit* subtetragonal, ca. 4 mm long and 5 mm wide, plainly 4-lobed, wrinkled in drying, 4-seeded; fruiting-calyx much enlarged and indurated, shallowly cupuliform or patelliform, deeply and irregularly lobed.

In forest and thickets from southern Mexico to Panama.

"Chiploque," "Taco," and "Taquito."

BOCAS DEL TORO: Changuinola Valley, *Dunlap 26* (F); *Stork 26* (US). Bocas del Toro, *von Wedel 683* (MO). Edge of river and railway and adjacent rainforest, Changuinola to 5 mi, S at junction of Río Changuinola and Río Terebé, 100–200 ft, *Lewis et al. 857* (MO). Boca de Zholquin, Talamanca, *Pittier 8643* (BR, US). Talamanca, *Tonduz 8627* (BR, US),

9292 (BR, US), *9293a* (G). Forest, Shirores, 100 m, *Tonduz 9293* (BR, US). Near Chiriquí Lagoon, *von Wedel 1351* (MO). Water Valley, near Chiriquí Lagoon, *von Wedel 1836* (NY). CANAL ZONE: Barro Colorado Island, *Ebinger 243* (MO). COCLÉ: Behind pension at El Valle, *Ebinger 954* (MO). PANAMÁ: Open grazed area near Jenine along Pan-American Highway, *Duke 3805* (MO, US).

11. **Aegiphila magnifica** Moldenke, Feddes Repert. 33: 132. 1933.

Shrub or woody *vine* to 6.5 m tall; branchlets robust, acutely tetragonal, distinctly canaliculate or sulcate, somewhat verruculose, light-brown, densely puberulent, with numerous prominent and irregularly disposed lenticels; bark mottled with light and dark blotches; leaf-scars large, circular on elevated sterigmata. *Leaves* opposite or approximate; chartaceous, entire, broadly oblong, 14–20 cm long and 8–10 cm wide, short-acuminate, basally abruptly acute or subacuminate, light-green and shiny, finely and obscurely puberulent on both surfaces, especially along the midrib and larger veins; petioles to 15 mm long, puberulent, sometimes verruculose. *Inflorescences* axillary cymes and terminal panicles, the cymes solitary, opposite, many-flowered, trichotomous, bracteolate, the panicles pyramidal-thyrsoid, often large and leafy, to 33 cm long and 30 cm wide at the base (in fruit), the sympodia elongate, stout, tetragonal, canaliculate, puberulent, often blotched and verruculose, the branches often distinctly approximate or subopposite, the lowermost fully 11 cm long, axillary to large, foliaceous bracts, which are smaller upwards; bracts large and foliaceous, caducous, leaving large scars below the branches of the terminal fruiting thyrse; bractlets and prophylls linear. *Flowers* with the corolla yellow. *Fruit* tetragonal, ovoid, yellow or orange, ca. 7 mm long and 6 mm wide, smooth, drying flattened and apically deeply umbilicate, 4-seeded, when mature the lower ⅓ loosely, if at all, invested by the fruiting calyx, fruiting peduncles 2–7 cm long, puberulent; fruiting pedicels stout, ca. 3 mm long, tetragonal, ampliate to ca. 2 mm, puberulent and often verruculose; fruiting calyx greatly enlarged and indurated, cupuliform, ca. 4 mm long and 9 mm wide, basally flat and truncate, puberulent, roughened and glabrate in age, apically scarious, entire or slightly repand, shallow, usually not closely investing the fruit.

In damp thickets from Guatemala to Panama.

BOCAS DEL TORO: Water Valley, *von Wedel 745* (MO). Without locality, *von Wedel 336* (MO). PANAMÁ: Moist thickets, Tumba Muerto Road, near Panamá, *Standley 29797* (AAH, US).

11a. **Aegiphila magnifica** var. **pubescens** Moldenke, Phytologia 3: 261. 1950.

This variety differs from the typical variety in the leaf-blades being densely pubescent or puberulent on both surfaces even when quite mature.

In cloud-forest clearings, Costa Rica and Panama.

CANAL ZONE: Near Gatuncillo, *Piper 5616* (NY, US).

12. **Aegiphila filipes** Mart. & Schau. *ex* Schau. *in* DC., Prodr. 11: 652. 1847.

Shrub, or *tree* to 7 m tall, sometimes subscandent; stems to 2.5 cm in diameter; branches slender and weak, obtusely tetragonal or subterete, greyish-scurfy, minutely puberulent or glabrous with scattered elevated lenticels; branchlets

slender, coarsely angular or subterete, slightly compressed at the nodes, brownish, minutely puberulent to pulverulent or glabrous. *Leaves* opposite; very thin-membranous and fragile when dry, oblong to elliptic, 8–18 cm long and 2–7.5 cm wide, mostly acuminate or abruptly acute (rarely obtuse), basally acuminate, entire or coarsely angulate-dentate above the middle, dark-green above, pale beneath, minutely puberulent on both surfaces especially along the midrib and veins, sometimes somewhat velvety to touch, in age becoming glabrous and shiny above and merely densely punctate beneath, marked with black glandular disks along the midrib beneath, the venation extremely delicate; petioles slender and very weak, 5–7 mm long, minutely puberulent or glabrate. *Inflorescences* axillary cymes and terminal panicles; the cymes axillary but mostly only toward the tips of the branchlets, bi- or trifid, ca. ⅓ as long as the subtending leaves, extremely weak and tenuous, loose and spreading, often drooping, loosely few-flowered; the panicle usually small, only 5–6 cm long and 4–6 cm wide, the branches few, slender, usually few-flowered, the sympodia few, short, slender, puberulent; peduncles slender or filiform, 1.2–5 cm long, minutely puberulent or pulverulent; pedicels filiform, weak, 2–9 mm long, puberulent; bractlets few, linear-lanceolate to subulate, 1–12 mm long, puberulent; prophylls minute. *Flowers* with the calyx campanulate or broadly cyathiform, 2.4–4 mm long and 3–4.2 mm wide, basally acute and attenuate into the pedicel, lax around the corolla-tube, minutely puberulent, subtruncate, 4-mucronulate or sinuate; corolla yellow or white, glabrous, infundibular or hypocrateriform, the tube narrow-cylindric, gradually ampliate above, 3–6 mm long, the lobes 4, linear-lanceolate or oblong to ovate-lingulate, 4–6 mm long and 2–3 mm wide, obtuse; stamens 4, inserted ca. 1 mm below the mouth of the corolla-tube, subincluded in the pistillate flowers or long-exserted in the staminate, the filaments 1–19 mm long, puberulent or glabrous; pistil included in the staminate flowers or exserted in the pistillate, the style 1.2–7.5 mm long, glabrous, the stigma branches divaricate, 1.8–2.6 mm long, the ovary globose or obovate, ca. 1.3 mm long and 1 mm wide, basally acute, flattened above, 4-lobed and 4-sulcate, glabrous, 4-celled. *Fruit* subglobose or oblong, 8–9 mm long, ca. 8 mm wide, yellow or orange, apically flattened and somewhat depressed, strongly and conspicuously lobed, wrinkled in drying, 1–4 seeded; fruiting-calyx cupuliform, greatly enlarged and indurated, ca. 6 mm long and 9 mm wide, subentire to deeply lobed or irregularly split.

In forests, damp woods, old clearings, and pastures, ranging from Panama to Amazonian Brazil, Peru, and Bolivia.

"Chirarapa-sacha."

DARIÉN: 1–3 mi. SW of Santa Fé, Río Sabana, *Duke 4114* (MO). PANAMÁ: Corozal Road near Panamá, *Standley 26853* (US).

13. **Aegiphila mollis** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 203, *pl. 130.* 1817.

A. mutisii H. B. K., loc. cit. 2: 203, *pl. 131.* 1817.
A. salutaris H.B.K., loc. cit. 2: 202. 1817.
A. mutisii var. *grandiflora* Schau. *in* DC., Prodr. 11: 654. 1847.
Cornutia velutina Hayek, Bot. Jahrb. Syst. 42: 172. 1908.

Shrubs or small *tree* to 5 m tall, often with a disagreeable or nauseous odor; trunk to 15 cm in diameter; bark grayish, rugose; branches obsoletely tetragonal

or subterete, stout, hirsute-lanate or tomentose becoming fuscous in age; branchlets obtusely tetragonal, mostly hirsute. *Leaves* opposite; chartaceous, usually drying dark, obovate-oblong or ovate-elliptic to elliptic, 6–19 cm long and 2–8.5 cm wide, attenuate-acuminate or acute, entire or with a few coarse, remote teeth above the middle, basally acute or acuminate and often narrowed into the petiole, sometimes inequilateral, mostly hirtellous above, more densely and softly canescent- or flavescent-pubescent beneath, the larger venation usually conspicuous beneath by its dense and divergent pubescence; petioles weak, 4–11 mm long, mostly densely pubescent. *Inflorescences* axillary cymes and terminal panicles, the cymes solitary, opposite, corymbose or paniculate, trifid-dichotomous, many-flowered, bracteate, ⅓–½ as long as the subtending leaves, divergent, sometimes gradually diminishing in size into the terminal panicle; the panicles thyrsoid, pyramidal or conic, to 17 cm long and 10 cm wide, often trichotomous, bracteate and foliose below, sometimes naked above, the sympodia tetragonal, decussately flattened at the nodes, fastigiate, densely pubescent, the branches divaricate, opposite or sometimes crowded, dichotomous, densely pubescent; peduncles terete or tetragonal, 1–5.5 cm long, densely yellowish-pubescent; pedicels 1–3 mm long, slender, pubescent; bracts large and foliaceous in pairs at the branches of the thyrse, lanceolate, stipitate, ca. 2 cm long and 6 mm wide, acute at both ends, sparsely pubescent on both surfaces; bractlets narrow or setaceous, 5 mm long; prophylls linear, minute. *Flowers* fragrant; calyx campanulate, 2–3.3 mm long and ca. 3.6 mm wide, subquadrangular, basally acute, veiny, densely pubescent outside, lax around the corolla-tube, subtruncate, repand or 4-mucronulate with short acute mucros; corolla infundibular or hypocrateriform, white to yellow, the tube narrow-cylindric, 3.7–5.3 mm long, much ampliate above, the lobes 4, oblong or sometimes ovate-elliptic, ca. 4 mm long and 2 mm wide, pilose outside, acute or subacuminate; stamens 4, inserted ca. 1.3 mm below the mouth of the corolla-tube, long exserted in the staminate flowers, equaling the corolla-tube or included in the pistillate, the filaments 1–10 mm long, slightly compressed, pilose; pistil included in the staminate flowers or long-exserted in the pistillate, the style 1–8.7 mm long, glabrous, the stigma branches 1–4 mm long, the ovary subrotund or ovate, ca. 0.8 mm long and wide, apically flattened and 4-lobed, glabrous, 4-celled. *Fruit* oblong or obtusely ovate, orange, 2–4-seeded; fruiting-calyx greatly enlarged and indurated, cupuliform, pronouncedly tetragonal, truncate.

In dense forests and other woodlands, along streams, and on llanos from Panama to Bolivia.

In some parts of its range it is used internally as a remedy against venomous snake bites and externally on wounds. "Contraculebra," "totumillo."

CHIRIQUÍ: Pastures around Boquete, *Pittier 2950* (US). Boquete, Boquete District, 3800 ft, *Davidson 638* (F, MO, US). Along road between Boquete and Cerro Horqueta, *Duke 13706a* (NY). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1174* (F, MO, NY). Near Boquete, 1200–1500 m, *Woodson & Schery 758* (MO, NY). COCLÉ: In thickets, Río Hato Military Reservation along the Interamerican Highway, *Tyson & Blum 2552* (MO). VERAGUAS: Veraguas, *Duke 12363* (BMIC). San Francisco, *Dwyer 1301* (M).

14. **Aegiphila hirsutissima** Moldenke, Feddes Repert. 33: 127. 1933.

Shrub or coarse *vine*; wood soft; branches and branchlets obtusely tetragonal

or subterete, slight flattened at the nodes, densely or sparsely setose or long-hirsute, the hairs coarse, brownish, to 3 mm long, distinct, erect, deciduous and leaving small glandular dots on the branches; leaf-scars circular on elevated sterigmata. *Leaves* opposite; membranous, mostly fragile and drying dark above, lighter beneath, oblong-lanceolate to oblong or obovate, 6.5–15 cm long and 2.5–7 cm wide, entire, acute or rounded (juveniles acuminate), basally acute and somewhat narrowed into the petiole in juveniles, apparently rounded or subtruncate at maturity, densely setose on both surfaces, the hairs lax, spreading, brownish, 1–4 mm long, ca. 1 mm apart, basally enlarged, denser along the larger veins and on younger leaves; petioles 3–9 mm long, densely setose. *Inflorescences* axillary cymes and terminal panicles, the cymes few, solitary, opposite, dense-flowered, ca. 4 cm long and 3.5 cm wide, subovate, later somewhat divaricate, the panicles pyramidal-thyrsoid to 11 cm long and wide during anthesis, dense-flowered, bracteate with greatly abbreviated sympodia, in fruit often narrow and elongate, 12–15 cm long and ca. 5 cm wide throughout, pendent, the branches ca. 14 pairs, short, few-fruiter; peduncles slender, 1.5–4 cm long, setose; pedicels slender, ca. 2 mm long, to 10 mm long in fruit, setose; bracts numerous, lanceolate, ca. 15 mm long, often concealed during anthesis by the densely congested flowers; bractlets linear, 5–8 mm long; prophylls setaceous. *Flowers* with the calyx campanulate or broadly obconic, lax around the corolla-tube, ca. 3.6 mm long and wide, densely setose with white divaricate hairs 2–2.5 mm long, subtruncate, 4-apiculate; corolla infundibular, the tube narrow-cylindric, ca. 5.4 mm long, ampliate above, glabrous outside, pilose in the throat, the lobes 4, oblong-lingulate, ca. 3.3 mm long and 2.6 mm wide, glabrous; stamens 4, inserted ca. 4.3 mm from the base of the corolla-tube, included in the pistillate flowers, the filaments about 0.8 mm long, densely pilose; pistil long exserted in the pistillate flowers, the style ca. 8.6 mm long, the stigma branches light, ca. 5.2 mm long, the ovary oblong, ca. 1 mm long and wide, depressed at both ends, glabrous, distinctly 4-lobed apically. *Fruit* yellow or orange, 15–18 mm long and wide, tetragonal, thick and fleshy, smooth, apparently 4-seeded, fruiting-calyx cupuliform, incrassate and coriaceous, ca. 4 mm long and 9 mm wide, veiny, loosely setose, basally narrow, entire.

Dense forest from southern Panama to Venezuela.

SAN BLAS: *Duke & Bristan 351* (BMIC).

15. **Aegiphila elata** Sw., Prodr. 31. 1788.

Nuxia elata (Sw.) Pers., Syn. Pl. 1: 132. 1805.
Omphalococca cornifolia Willd. *in* Roem. & Schult., Mant. 3: 132. 1827.
Psychotria mollis Spreng. *in* DC., Prodr. 4: 513. 1830.
Aegiphila cornifolia (Willd.) Kunth, Abh. Königl. Akad. Wiss. Berlin 215. 1831.

Branching *shrub* or woody *vine*, sometimes trailing, often high-climbing, 2–8 m tall; stem to 8 cm in diameter; branches elongate, stout; branchlets slender, obtusely tetragonal, glabrous or minutely puberulent toward the tips. *Leaves* opposite; firmly chartaceous, not blackening or becoming fragile, entire, ovate to elliptic, 7–20 cm long and 2.5–9 cm wide, abruptly attenuate or narrowly acuminate, basally blunt or rounded, rarely subcordate, dark-green and glabrous above, paler beneath, shiny, and appressed-pubescent on the midrib and larger

veins beneath, glabrescent and often thinly glandular punctate in age; petioles 5–12 mm long, often much thickened basally, puberulent. *Inflorescences* axillary cymes and terminal panicles; the cymes ca. ⅓–½ as long as the subtending leaves, opposite, solitary, many-flowered, usually quite distinct from the panicle; the panicles corymbose or thyrsoid, about 16 cm long and 11 cm wide, erect, usually naked; peduncles 1–4 cm long, often flattened and ampliate above, minutely puberulent or glabrate; pedicels slender, 4–8 mm long, puberulent. *Flowers* with the calyx turbinate-infundibular to cupuliform, usually basally acute and ventricose or constricted above the ovary, 2–4 mm long and 2.6–4.2 mm wide, firm, lax around the corolla-tube, puberulent or pubescent, apically membranous, distinctly 4-lobed, dilated, the lobes ovate, erect, retuse or mucronulate; corolla yellowish or cream-colored to white, infundibular or hypocrateriform, the tube cylindric, slender, 4–8 mm long, the lobes usually 4, oblong- or elliptic-lingulate, 3–6 mm long and ca. 3.7 mm wide, spreading, obtuse; stamens 4, inserted ca. 3.5 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers or included in the pistillate, the filaments 0.3–7 mm long, glabrous; pistil long-exserted in the pistillate flowers or included in the staminate, the style 2–4 mm long, the stigma branches 2–4.5 mm long, the ovary subrotund, dark, ca. 0.9 mm long and wide, flattened above. *Fruit* subglobose or subtetragonal, 7–10 mm long and wide, flattened at both ends, firm, yellow or orange, 3- or 4-seeded, when immature almost included in the calyx, semi-included when mature, often borne in large clusters 10–15 cm long; fruiting-calyx greatly enlarged and indurated, cupuliform, ca. 5 mm long and 6–10 mm wide, roughened, glabrate, shallowly and irregularly lobed or sometimes deeply split.

Margins of woods, hedges, thickets, and borders of streams, ranging from Cuba and Mexico through the West Indies and Central America to Colombia, Venezuela, and the Guianas.

"Bejuco de peine mico," "guairo santo," "guaro" (Spanish), "spirit-weed" (English).

CANAL ZONE: Barro Colorado Island, *Croat 5506* (AAU, NY). COLÓN: East Ridge, in tropical wet forest, *Duke 15269* (BMIC). DARIÉN: Cerro Pirre, *Bristan 592* (MO, SRGH). PANAMÁ: Cana and vicinity, 2000–6500 ft, *Williams 829* (NY, US).

16. **Aegiphila hoehnei** var. **spectabilis** Moldenke, Castanea 10: 44. 1945.

Subscandent *shrub* or *vine*; branches slender, obtusely tetragonal, densely but often irregularly villose with gray antrorse hairs of various lengths; branchlets slender, obtusely tetragonal, densely ochraceous-villous with straight antrorse hairs 1–2 mm long and bulbous-based; internodes mostly elongate. *Leaves* opposite; firmly chartaceous or subcoriaceous, ovate, 8–12.5 cm long and 3.7–6 cm wide, entire, acuminate, basally cordate, mostly drying bullate above, bright-green, somewhat lighter beneath, shiny and setose above with stiff hairs 1–2.5 mm long and conspicuously bulbous-based, densely villous beneath with ochraceous hairs 2–3 mm long and not bulbous, densest on the venation, densely punctate beneath, at least the larger venation drying conspicuously impressed above and sharply prominulent beneath; petioles stout, 5–8 mm long, densely long-villous. *Inflorescences* axillary cymes and terminal panicles, the panicles

cymose and similar to the cymes; the cymes few, solitary, opposite, abbreviated, ca. 3 cm long and 2.5 cm wide, to 4.5 cm long and 5 cm wide in fruit, many-flowered; peduncles stout, to 1.5 cm long, densely villous with ochraceous or fulvous antrorse hairs. *Flowers* with the calyx infundibular, 8–10 mm long, ca. 4.6 mm wide, narrow to just above the ovary then ampliate, densely setose-villous with hairs to 2 mm long, deeply 4-lobed, the lobes ca. 2.6 mm long and 2 mm wide, ovate, rounded and subcucullate, setose; corolla greenish-white or white to yellow, hypocrateriform, the tube narrow-cylindric, at least 7.2 mm long, glabrous; style at least 7 mm long, the ovary subtetragonal, ca. 1.5 mm long and wide, truncate at both ends, glabrous. *Fruit* oblong, yellow-orange, 13–16 mm long and 9–10 mm wide, glabrous, slightly verruculose in drying, not shiny, 4-seeded; fruiting calyx large and incrassate, cupuliform, to 1.5 cm long and 1.8 mm wide, externally villous-setose, deeply 4-lobed, the lobes triangular-ovate and about 7 mm long.

In forests, Panama and Colombia.

PANAMÁ: Summit of Cerro Jefe and forests beyond, *Hayden 1003* (MO, US). Top of Cerro Jefe, 2700–3000 ft, *Tyson et al. 4342* (MO).

17. **Aegiphila deppeana** Steud., Nom., ed. 2. 1: 29. 1840.

A. brachiata Schlecht. & Cham., Linnaea 6: 371. 1831, non *A. brachiata* Vell., Fl. Flum. 38. 1825.

Diffuse *shrub* or small *tree*, 2.5–7 m tall, or loosely twining *vine*; branches obtusely tetragonal or subterete, grayish-brown, shortly and densely cano-tomentose, glabrescent, the margin with numerous prominent lenticels; branchlets diffuse, obsoletely tetragonal or terete, somewhat compressed at the nodes, softly and densely fulvo-pubescent, the hairs mostly erect. *Leaves* opposite; chartaceous or when older subcoriaceous, ovate or oblong-ovate, 5–16 cm long and 2–9 cm wide, entire, acute or acuminate to short-cuspidate (very rarely rounded), basally acute or subcuneate, rarely obtusely rounded, sometimes slightly oblique, grayish-green, shiny, glabrate above except for the midrib and secondary veins, softly and densely cano-tomentose beneath, especially along the midrib and secondaries or in age rarely glabrate; petioles 4–13 mm long, densely fulvo-pubescent. *Inflorescences* axillary cymes and terminal panicles; the cymes in the axils of the uppermost leaves, ca. ½ as long as the subtending leaf, many-flowered, bracteate and bracteolate; the panicles terminal, bracteate, often embracing the uppermost cymes, the branches mostly trichotomous, often ascending, incanous and lanuginous-tomentose; peduncles 1–4.5 cm long, subappressed-pubescent with buff or fulvous hairs; pedicels slender, ca. 3 mm long, similar to the peduncles in pubescence; bracts foliaceous, scattered or in pairs at the base of the panicle-branches, oblong, stipitate, ca. 2.5 cm long and 1.5 cm wide, glabrous above or somewhat pubescent along the midrib, tomentose beneath; bractlets and prophylls narrowly linear or setaceous, ca. 1 mm long, tomentose. *Flowers* with the calyx obconic-campanulate, ca. 4 mm long and 2.5 mm wide, densely subappressed-pubescent with incanous or fulvous hairs, 4-dentate or 4-lobed, the lobes ovate, obtuse and mucronulate or submucronulate, broader than long; corolla white or pale-yellow, glabrous, infundibular, the tube cylindric, slender, 5–12 mm long, gradually

ampliate above, the lobes 4, elliptic or oblong-elliptic, ca. 4 mm long and 2.5 mm wide, obtuse; stamens 4, inserted ca. 1.8 mm below the mouth of the corolla-tube, long-exserted in the staminate flowers or included in the pistillate, the filaments 0.5–7.5 mm long, glabrous or slightly pubescent below; pistil exserted in the pistillate flowers or included in the staminate, the style 22.5–8 mm long, the stigma branches 3–6.5 mm long, the ovary ovoid, flattened, about 0.9 mm long and 1 mm wide, glabrous. *Fruit* obovoid, subtetragonal, flattened at both ends, 8–10 mm long and 6–8 mm wide, yellow, roughened, slightly or greatly inclosed by the fruiting-calyx; fruiting-calyx cupuliform, greatly enlarged and indurated, ca. 1 cm wide, roughened, tomentose, irregularly and shallowly lobed.

In thickets and llanos and at the edge of paths from Mexico to French Guiana.

"Sauco de monte," "sauco monte."

CHIRIQUÍ: Near David, *Pittier 2842* (US). Chiriquí and Veraguas, *Wagner*, 1858 (M). LOS SANTOS: Gravel riverbed and forest edge, Río Tonosí, near Tonosí, *Lewis et al. 1559, 1566* (both MO, US). Near Tonosí, along Quebrada Ocho Paso, a small tributary of the Río Tonosí, *Stern et al. 1828* (MO, US). Between Tonosí and Guanico, *Stern et al. 1876* (MO, US). 1 mi. N of Tonosí, *Tyson et al. 2988* (MO). Bank of river, Tonosí, *Tyson et al. 3100* (MO). VERAGUAS: Without locality, *Seemann 1202* (BM, K). Veraguas, *von Warscewicz 7* (B).

11. CALLICARPA

Callicarpa L., Sp. Pl. 111. 1753; Gen. Pl., ed. 5. 50. 1754.

Burchardia Heist. *ex* Duham., Traité Arbres & Arbustes 1: 111, *pl. 44*. 1755.
Johnsonia T. Dale *ex* Mill., Gard. Dict., ed. 7. 1759.
Illa Adans., Fam. Pl. 2: 446. 1763.
Porphyra Lour., Fl. Cochinch., ed. 1. 1: 60. 1790.
Amictonis Raf., Sylv. Tellur. 161. 1838.

Trees or *shrubs*. *Leaves* mostly decussate-opposite, simple, deciduous, exstipulate. *Inflorescences* cymose (determinate), axillary or supra-axillary; usually polygamous. *Flowers* actinomorphic; calyx gamosepalous, tubular or campanulate to cyathiform, 4-fid to 4-toothed, sometimes entire, rarely 5-toothed; corolla gamopetalous, infundibular or hypocrateriform, the tube straight, usually broadly cylindric, ampliate above, the limb 4-(rarely 5-)parted, the lobes lingulate, isomorphic, spreading; stamens 4 or rarely 5, equal, inserted at or near the base of the corolla-tube, alternate with the corolla-lobes, usually more or less exserted, the filaments filiform, separate, glabrous, the anthers oblong or elliptic, dorsifixed near the base, 2-celled, the thecae parallel and opening extrorsely by longitudinal slits or rarely by terminal pores; pistil single, terminal, compound, absent from staminate flowers, the style single, capillary, glabrous, the stigma depressed-capitate or peltate, the ovary single, compound, usually subglobose and more or less pubescent, 4-celled, of 2, 2-celled carpels, each cell with 1-high-lateral ovule, rudimentary or absent in staminate flowers. *Fruit* drupaceous, more or less globose or depressed-globose with fleshy and variously colored exocarp and hard endocarp, the latter separating into 4, (or through abortion fewer) stoney pyrenes, each containing a single seed; embryo straight, with scanty or no endosperm; fruiting-calyx usually unchanged, patelliform.

A complex genus of about 205 specific and infraspecific entities, widely distributed in tropical and subtropical America, Asia and Oceania, a few species ranging into temperate Asia and America.

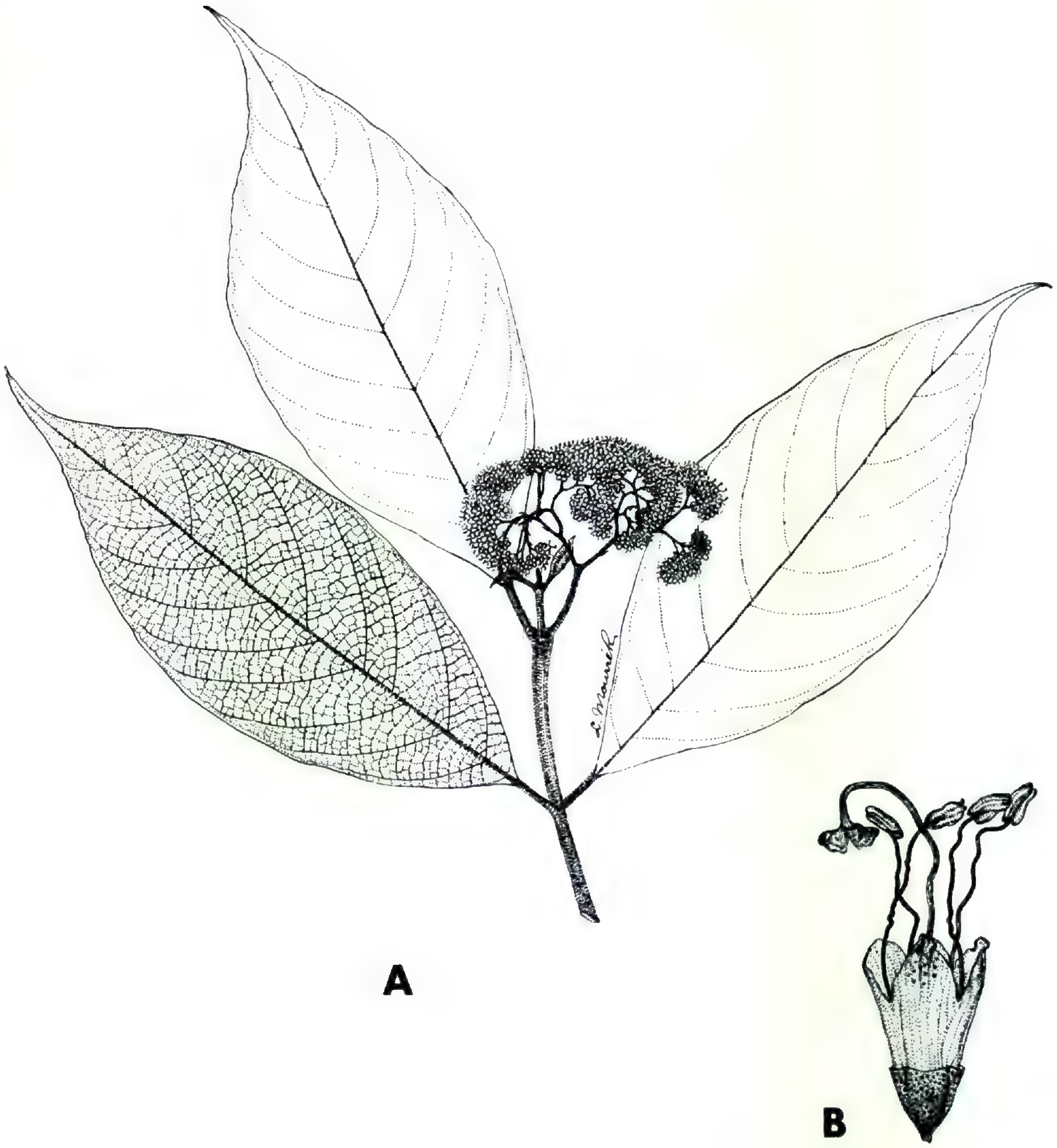

FIGURE 11. *Callicarpa acuminata* H.B.K.—A. Habit (× ⅜).—B. Flower (× 7½). [After *von Wedel 1895* (MO).]

1. **Callicarpa acuminata** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 204. 1817.—FIG. 11.

C. subintegerrima H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 204. 1817.
C. bonplandiana Schult., Mant. 3: 50. 1827.
C. schlimii Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 217–218. 1863.

Shrub or *tree* to 10 m tall; trunk to 12 cm in diameter; branches usually stout, obtusely tetragonal, densely stellate floccose-tomentose above, more or less glabrescent, with numerous elongated lenticels; branchlets and twigs from stout to slender, obtusely tetragonal, flattened at the nodes, usually densely floccose-tomentose with whitish or yellowish tomentum, later becoming less so. *Leaves* membranous, ovate-oblong or very rarely subobovate, 6.5–28.5 cm long and 2.5–

11.5 cm wide, entire or subentire to sharply serrate, except basally, apically acute or acuminate and often narrowed to an elongate acumen, basally acute or acuminate, often somewhat narrowed into the petiole, dark-green above, much lighter beneath, more or less stellate-furfuraceous above, especially along the midrib and larger veins, and more or less glabrescent, densely stellate-tomentose and glandular-punctate or furfuraceous-floccose beneath; petioles stout, 6–28 mm long, very densely floccose-tomentose. *Inflorescences* solitary, opposite, cymes chiefly in the uppermost axils, often laxly corymbose and greatly branched, usually long-pedunculate, 2.5–20 cm long and 3–17 cm wide, usually many-flowered, frequently densely so, sometimes bracteate, bracteolate; peduncles stout, 1.5–6.5 cm long, densely floccose or furfuraceous with flavescent or canescent tomentum; pedicels slender, 1–3 mm long, densely canescent-tomentose; bracts (if present) subfoliaceous, oblong, to 3.5 cm long and 1 cm wide, stellate-tomentose; bractlets linear, often numerous, 5–10 mm long, densely canescent-tomentose; prophylls setaceous. *Flowers* slightly fragrant, calyx small and thin-textured, 1.1–1.5 mm long and wide, often 4-angled and 4-costate, granulose-pulverulent, truncate or subtruncate, often very slightly 4-dentate or irregularly erose; corolla white or greenish-white, infundibular, the tube 1.6–2.6 mm long, the limb 4-parted, the lobes short, ovate-lingulate, 0.8–0.9 mm long and 0.9–1 mm wide, apically bluntly obtuse, sometimes slightly crimped or bilobed; stamens 4, inserted at the base of the corolla-tube, long-exserted, the filaments 3.1–7.6 mm long, the anthers oblong; pistil absent or long-exserted, the style 4.2–7 mm long, ampliate into the stigma, the stigma depressed-capitate, ca. 0.9 mm wide; ovary depressed-globose, ca. 0.6 mm long and wide, 4-sulcate, glabrous. *Fruit* dark-purple or almost black, subglobose, 3–4.5 mm long and wide, glabrous, drying wrinkled, 4-seeded, whitish-lavender to yellow or red when immature; fruiting-calyx small, shallowly patelliform, 2–3 mm wide, glabrate, truncate and entire.

Lowland thickets, gravel bars, seacoasts, as well as forest and rainforests ranging from Mexico to Bolivia.

The species is quite variable in leaf-size and texture and in the density of the pubescence.

BOCAS DEL TORO: Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2017* (MO, US). Coast, Columbus Island, *von Wedel 31* (MO, US). Colón Island, *von Wedel 71, 167, 218* (all MO). Water Valley, Chiriquí Lagoon, *von Wedel 1627* (MO), *2666* (MO, US). Old Bank Island, Chiriquí Lagoon, *von Wedel 1895* (MO). Snapper Creek, Chiriquí Lagoon, *von Wedel 2641* (MO). Water Valley, Big Bight, Chiriquí Lagoon, *von Wedel 2980* (MO). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2488* (US). Forest behind Club Campestre, 700 m, *Duke 13266* (MO). DARIÉN: Between Quebrada Venado and Peje Swamp, headwaters of Río Tuqueza, *Bristan 1015* (MO, N, US). Río Mortí, ca. 6 mi. upstream from Mortí Abajo, 100 m, *Duke 10152* (MO). Río Mortí, Camp Mortí Abajo, *Duke 14120* (MO). Mortí Hydro, 260 m, *Duke 14240* (MO). Río Tuira between Río Punusa and Río Mangle, *Duke 14612* (MO). Around Garachine, *Pittier 5520* (US). PANAMÁ: San José Island along road between Bodega Bay and Río Mata Puerco, *Duke 12515* (MO). Gravel bar, Río Cañasas, 100 m, *Duke 14512* (MO). Open places along road near headquarters, San José Island, *Erlanson 5* (US). Abundant in thickets, Main Camp, San José Island, *Johnston 6* (MO). Near village, Saboga Island, *Tyson 5580* (MO). SAN BLAS: Permé, *Cooper 220a* (US). Soskatupo Island, *Duke 8515* (MO). Nakka, *Dwyer 6877* (FT, MO). Soskatupu Island, *Elias 1663* (MO). Mainland opposite Achituppu, *Lewis et al. 115* (MO).

12. TECTONA

Tectona L. f., Suppl. 20: 151. 1781.

Theka Adans., Fam. Pl. 2: 445. 1763, nom. rejic.
Nautea Noronha, Verh. Batav. Genootsch. Kunsten V, ed. 1, art. 4: 3. 1790.
Tectonia Spreng., Anleit. 2: 893. 1818.

Tall *trees* with soft bark and more or less tetragonal branches and branchlets. *Leaves* deciduous, petiolate or subsessile, mostly large and broad, entire or denticulate, decussate-opposite or ternate. *Inflorescences* cymose, the cymes numerous, many-flowered, borne in massive terminal panicles and sometimes smaller axillary cymes in the upper leaf-axils. *Flowers* actinomorphic; calyx gamosepalous, campanulate, shortly 5–7 lobed, persistent, in fruit greatly enlarged and often inflated, enveloping the fruit and closed above it; corolla gamopetalous, hypocrateriform, white or blue, the tube short cylindric, the limb patent or reflexed, 5–7-parted, the lobes subequal, overlapping in bud; stamens 5 or 6, inserted in the corolla-tube, equal, exserted, the anthers ovate or elliptic-oblong, 2-celled, dorsifixed, the thecae parallel-opening by longitudinal slits; pistil single, elongate, the style terminal, capillary, the stigma very shortly bifid, its branches subequal, the ovary compound, 2-carpellate, completely 4-celled (each carpel 2-celled), each cell 1-ovulate, the ovules lateral or high-lateral, hemianatropous. *Fruit* drupaceous, rounded or weakly 4-lobed, completely enveloped by the enlarged fruiting-calyx with a thin subcarneous exocarp, a thick bony 4-celled endocarp, and a small central cavity between the cells; seeds without endosperm.

A small but commercially important genus of 5 specific and infraspecific taxa native to southern and eastern Asia, widely cultivated elsewhere.

1. **Tectona grandis** L. f., Suppl. 151. 1781.—Fig. 12.

T. theka Lour., Fl. Cochinch., ed. 1. 137. 1790.
Theka grandis (L. f.) Lam., Illustr. 2: 111. 1793.

Tree to 50 m tall; branches and branchlets stout, 4-sided, with large, quadrangular pith, the younger parts usually with obtuse angles and drying more or less sulcate between the angles, densely furfuraceous-tomentose with cinereous or ochraceous tomentum; nodes distinctly annulate with usually a corky layer and denser tomentum. *Leaves* drooping, deciduous, with a clasping base; firmly chartaceous, broadly elliptic, (11–)23–55(–85) cm long (to 1 m on turoins) but (6–)22–37(–50) cm wide, apically acute or short-acuminate, entire or repand-denticulate, basally abruptly acute or long-acuminate and prolonged into the alate petiole or clasping at the base, dark-green and shiny above, much lighter and not shiny beneath, densely squamose and rugose or bullate above, glabrescent and becoming smooth, densely furfuraceous-tomentose beneath with ochraceous or reddish to brownish hairs and densely resinous-punctate; petioles short or wanting, more or less margined or alate, densely ochraceous-furfuraceous. *Inflorescences* in the uppermost leaf-axils and terminal, paniculate, massive, the terminal panicles often many decimeters long and wide, but mostly ca. 40 cm long and 35 cm wide with distant, opposite, widely divaricate, many-branched, many-flowered cymes, densely cinereous- or ochraceous-furfuraceous throughout; peduncles and sym-

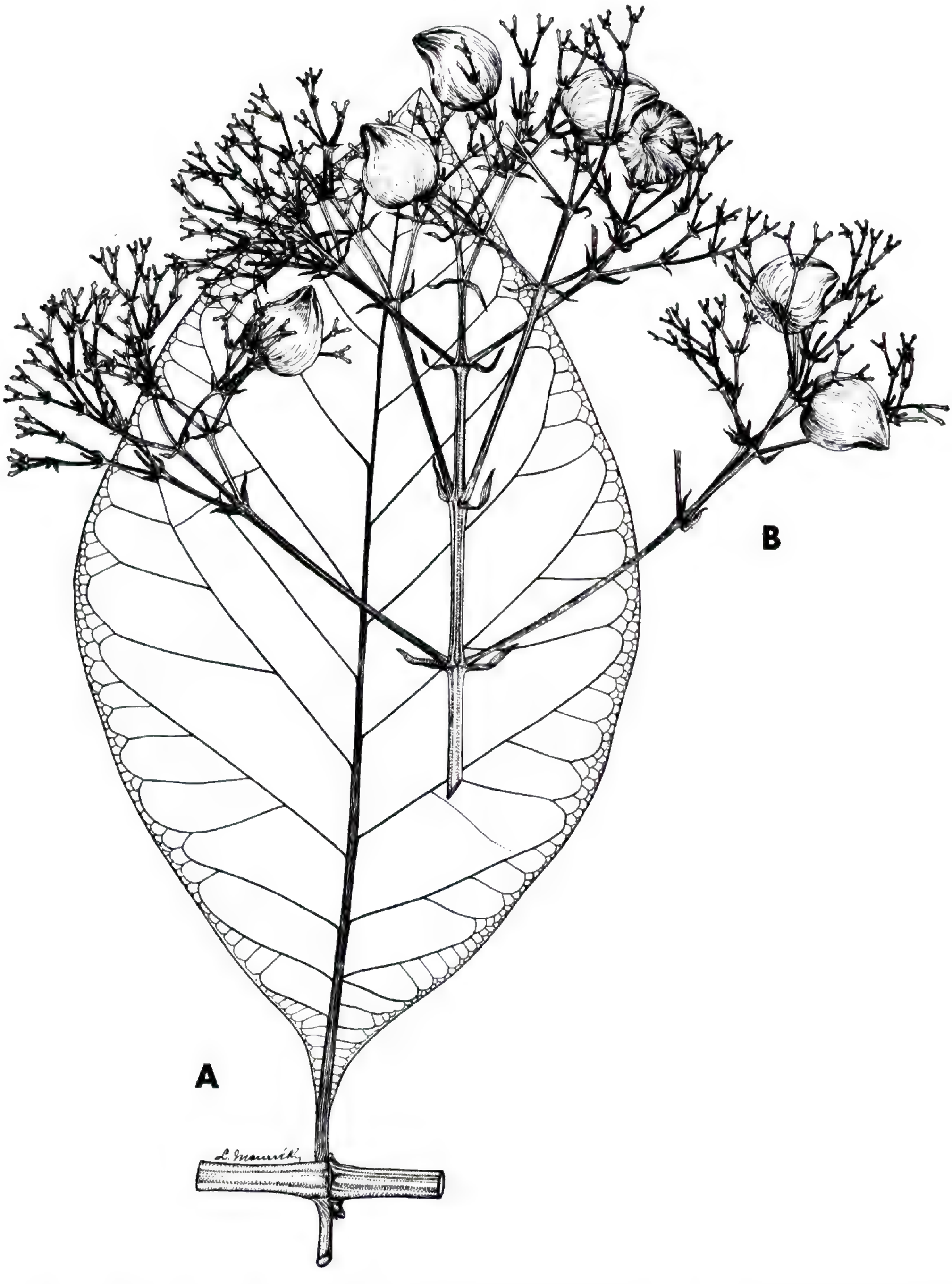

FIGURE 12. *Tectona grandis* L. f.—A. Leaf (× ¼).—B. Peduncle, pedicels, and fruits (× ½. [After *Tyson & Blum 2719.*]

podia continuous with the branchlets and similar in texture, color and pubescence, often elongate; pedicels stoutish or slender, 1–4 mm long, furfuraceous; a pair of large, foliaceous bracts subtending each pair of cymes, resembling the leaves but smaller; bractlets numerous, lanceolate-linear, to 15 mm long and 4 mm wide at

the base, sessile, ochraceous-furfuraceous, apically attenuate; prophylls oblong or linear-lanceolate, to 5 mm long and 1 mm wide. *Flowers* with the calyx light-yellow or light-green, 3–4.5 mm long and 3–3.5 mm wide, densely furfuraceous-tomentose, 5–7-toothed or -lobed, the teeth ovate or ovate-oblong, 1.5–2.5 mm long, often reflexed, obtuse; corolla white, sometimes rosy on the lobes, short-hypocrateriform, glabrous on both surfaces, the tube broadly cylindric, 1.5–3 mm long, ca. 1.5 mm wide, the limb 5–7-parted, the lobes obovate-elliptic, 2.5–3 mm long and ca. 2.3 mm wide, apically rounded, overlapping, erect or reflexed, inserted ca. 1.3 mm or more below the mouth of the corolla-tube, the filaments white, 2.5–4 mm long, glabrous, ampliate and flattened below, the anthers yellow, ovate or oblong; style white, 3.6–5.2 mm long, more or less pubescent with branched hairs, the ovary ovate or conic, 1.5–2 mm long, densely pubescent. *Fruit* subglobose or tetragonally flattened, to 1.5 cm long and wide, densely tomentose with irregularly branched light-brown or ochraceous hairs, umbilicate and 4-lobed at the apex; seeds oily; fruiting-calyx to 2.5 cm long and wide, chartaceous, light brown and brittle when dry, mostly irregularly plaited or crumpled and bladder-like.

Native to the tropics of southern Asiatic and Malayasia, especially abundant in the mixed forests of India, Burma, Thailand, and Malaya.

The species is widely cultivated for its timber and as specimen trees elsewhere. "Teak."

CANAL ZONE: Miraflores Annex, *Blum 682* (MO). Summit, *Mell 8* (NY). Miraflores in cultivation, *Moldenke 1231* (MEOW). Miraflores Lab near Locks, *Tyson & Blum 2791* (MO). Low jungle near Miraflores Lock, *Welch 19651* (MO).

13. CORNUTIA

Cornutia L., Sp. Pl. 628. 1753; Gen. Pl., ed. 5. 276. 1754.

Agnanthus Vaill., Hist. Acad. Roy. Sci. [Gall.]. 1722: 201. 1724.
Cornuta L., Gen. Pl., ed. 1. 366. 1737; ed. 6. 316. 1764.
Hosta Jacq., Hort. Schoenbr. 1: 60, pl. 114. 1797, non *Hosta* Tratt., Arch. Gewächsk. 2: 144. 1814, nom. cons.
Hostana Pers., Syn. Pl. 2: 143. 1806.

Odoriferous *trees* and *shrubs*, mostly pubescent or tomentose throughout, often glandular-punctate; branches and branchlets mostly rather stout, tetragonal, often margined; nodes mostly annulate, often conspicuously so. *Leaves* simple, decussate-opposite, exstipulate, deciduous, petiolate, mostly large and broad, pubescent. *Inflorescences* mostly terminal, large pyramidal-thyrsoid panicles, sometimes also axillary and cymose, the cymes not involucrate. *Flowers* small, zygomorphic, perfect; calyx mostly small, cupuliform or cyathiform to campanulate, obconic, or patelliform, slightly irregular when mature, mostly unchanged or shrivelled to a patelliform condition in fruit, during anthesis entire or minutely 4(or 5)-dentate, rarely lobed; corolla hypocrateriform, zygomorphic, blue or violet to purple or white, the tube cylindric, often inflated at the base, constricted at the middle, ampliate above, straight or slightly curved, the adaxial side longer, pubescent within and often outside, the limb patent, 2-lipped, 4-parted, the adaxial lip 3-lobed with subequal ovate- or elliptic-lingulate lobes overlapping in bud or

the central one outside, the abaxial lip composed of 1 lobe larger than the others and included by them in bud, made up of two distinct halves of which the upper is thinner, more glabrous, and folded in like a flap, the whole limb mostly pubescent inside and out; stamens 4, inserted in the corolla-tube at or above the middle, didynamous, the lower 2 fertile, longer, sometimes exserted, alternate with the largest corolla-lobe, the upper 2 reduced to filiform, mostly anantherous, included staminodes, the filaments flattened, mostly pubescent, the anthers 2-celled, dorsifixed, the thecae widely divergent basally, dehiscing by longitudinal slits, the connective much thickened; pistil 1, compound, mostly included, the style terminal, single, usually pubescent, of 2, 2-celled carpels, distinctly 4-celled, each cell with 1 high-lateral hemianatropous ovule; disk present beneath the ovary and about equalling it. *Fruit* drupaceous, small, abundant, subglobose, the exocarp fleshy, the endocarp hard and bony, the stones (1–3–)4-celled and -seeded; seeds without endosperm, the coat perforated at the base, stoney, rugose.

A difficult genus of 25 mostly variable and polymorphic species and infraspecific entities of the American tropics. Many are handsome when in flower. The named species and varieties are in many cases not clearly defined.

a. Branches, rachis, petioles and both leaf-surfaces short-pubescent, or pulverulent.
  b. Branches, branchlets, rachis, petioles, and lower leaf-surface densely short-pubescent.
    c. Flower-buds densely long hirsute ---------- 1b. *C. grandifolia* var. *normalis*
    cc. Flower-buds merely short-pubescent or strigose ---- 1a. *C. grandifolia* var. *intermedia*
  bb. Branches, branchlets, and rachis scattered pilose, pulverulent or glabrate.
    d. Leaves villous with long, glistening, white, multicellular hairs ---------- 2a. *C. microcalycina* var. *anomala*
    dd. Leaves short-pubescent or glabrate above, densely short-tomentose or pulverulent-puberulent beneath.
      e. Leaves densely or sparsely short-tomentose beneath ---------- 2. *C. microcalycina*
      ee. Leaves merely pulverulent or pulverulent-puberulent beneath ---------- 2b. *C. microcalycina* var. *pulverulenta*
aa. Branches, rachis, petioles and both leaf-surfaces long-pubescent, hirsute, villous, or tomentose ---------- 1. *C. grandifolia*

1. **Cornutia grandifolia** (Schlecht. & Cham.) Schau. *in* DC., Prodr. 11: 682. 1847.

Hosta grandifolia Schlecht. & Cham., Linnaea 5: 97. 1830.
H. grandiflora A. Dietr., Sp. Pl. 1: 252. 1831.
Cornutia grandiflora Steud., Nom., ed. 2. 1: 422. 1840.
C. pyramidata var. *dentata* Kuntze, Rev. Gen. 2: 506. 1891.

Shrub or *tree* to 8 m tall; branchlets stout, obtusely or acutely tetragonal, sometimes sulcate between the angles, occasionally 4-margined, densely villous-tomentose with spreading buff or brownish hairs, glabrescent, especially on the angles, often slightly swollen at the nodes, these marked with a band of longer and denser hairs. *Leaves* thin-membranous or chartaceous, elliptic or elliptic-ovate, 8.5–31 cm long, 6.5–19.2 cm wide, apically acuminate-entire, with short acute or acuminate teeth on the middle and upper portion, basally acuminate and prolonged into the petiole, dark green above, lighter beneath, more or less densely villous above with multicellular hairs, 1–2 mm long, or merely densely appressed-pubescent, beneath densely short-villous-pubescent with buff or brownish hairs;

petioles stout, 1–2.5 cm long, densely villous-tomentose. *Inflorescences* terminal and thyrsoid, sometimes with a few small axillary cymes in the uppermost leaf-axils, 15–42 cm long and 5–25 cm wide, many-flowered, the branches 1–3 times bifurcate, ultimately densely several-flowered; peduncles obsolete or to 2.5 cm long, similar to the branchlets; large and foliaceous bracts occasionally present; bractlets linear, 2–15 mm long and 1–3 mm wide; prophylls minute, setaceous, hidden by the dense pubescence; pedicels slender, 1–3 mm long; calyx patelliform or cupuliform, 1–1.5 mm long and 2.6–3.1 mm wide, densely short-pubescent, apically truncate and entire; corolla blue, violet, mauve, or purple, puberulent outside, except for the upper half of the abaxial lobe and pubescent within, the tube curved, the adaxial side ca. 8.8 mm long, the abaxial side ca. 7.8 mm long, basally swollen to 4.1 mm diameter, apically 2.8 mm wide at the apex, the abaxial lobe elliptic-lingulate, ca. 9.5 mm long and 4.3 mm wide, subacute, the adaxial lobes similar but smaller; ovary ca. 1 mm long and wide, densely hirsute. *Fruit* subglobose, fleshy, 3–4 mm long and wide, densely pubescent with spreading hairs; fruiting-calyx patelliform, ca. 1 mm long and 3 mm wide, densely pubescent, apically entire.

Lowland wet thickets and forest, fences, and roadsides, open woods, and in sandy soil mostly in secondary growth. Native from Mexico to Panama, this species is sometimes cultivated.

CANAL ZONE: Roadside, Chivi-Chivi Trail, 2 mi. above Red Tank, *Maxon & Harvey 6610* (US). COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1637, 1795* (both MO). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 537* (MO, NY, US). Cerro Pilón, hill below summit above El Valle de Antón, 2000–2700 ft, *Dwyer et al. 4571* (MO). Cerro Pilón, El Valle, *Kirkbride 1073* (MO). PANAMÁ: *Standley 26662* (US).

1a. **Cornutia grandifolia** var. **intermedia** Moldenke, Feddes Repert. 40: 167. 1936.

This variety differs from the typical variety in that the branchlets, petioles, leaf-blades, peduncles, sympodia, inflorescence-branches, pedicels, bracts, bractlets, prophylla, and calyces are merely very short-pubescent or puberulent. The fruit is also more sparsely pubescent with much shorter hairs or is only puberulent.

In rainforests or cloud-forests, low or moist thickets, riverbanks, and hedgerows from Guatemala to Panama.

BOCAS DEL TORO: Riverbank and beach, Santa Catalina, *Blackwell et al. 2757* (MEOW). Along riverbank, Cricamola, region of Almirante, *Cooper 529* (F, K, NY, US, YU). Rainforest by river, Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2016* (MO, US). Chiriquí Trail, near Chiriquí Lagoon, *von Wedel 2173* (MO). CANAL ZONE: Miraflores Locks area, *Tyson 1266* (MO). Curundu near tennis courts, *Tyson & Lazor 5430* (MO). COCLÉ: *Allen 4222* (MO). Cloud forest, mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1746* (MO, US). DARIÉN: Lucuti, Chepejana district, *Terry & Terry 1379* (MO). Cana and vicinity, 2500 ft, *Williams 963* (NY, US). PANAMÁ: Roadside near Chepo, *Dodge 10723* (MO, S). Panamá, *Seemann 257* (BM-in part); *Standley 25853* (US). VERAGUAS: 12 mi. from Santiago toward Divisa on the Transisthmian Highway, *Dwyer & Kirkbride 7246* (MO, US).

1b. **Cornutia grandifolia** var. **normalis** (Kuntze) Moldenke, Feddes Repert. 40: 170. 1936.—FIG. 13.

C. pyramidata var. *normalis* Kuntze, Rev. Gen. 2: 506. 1891.

This variety differs from the typical variety in the pubescence on the branch-

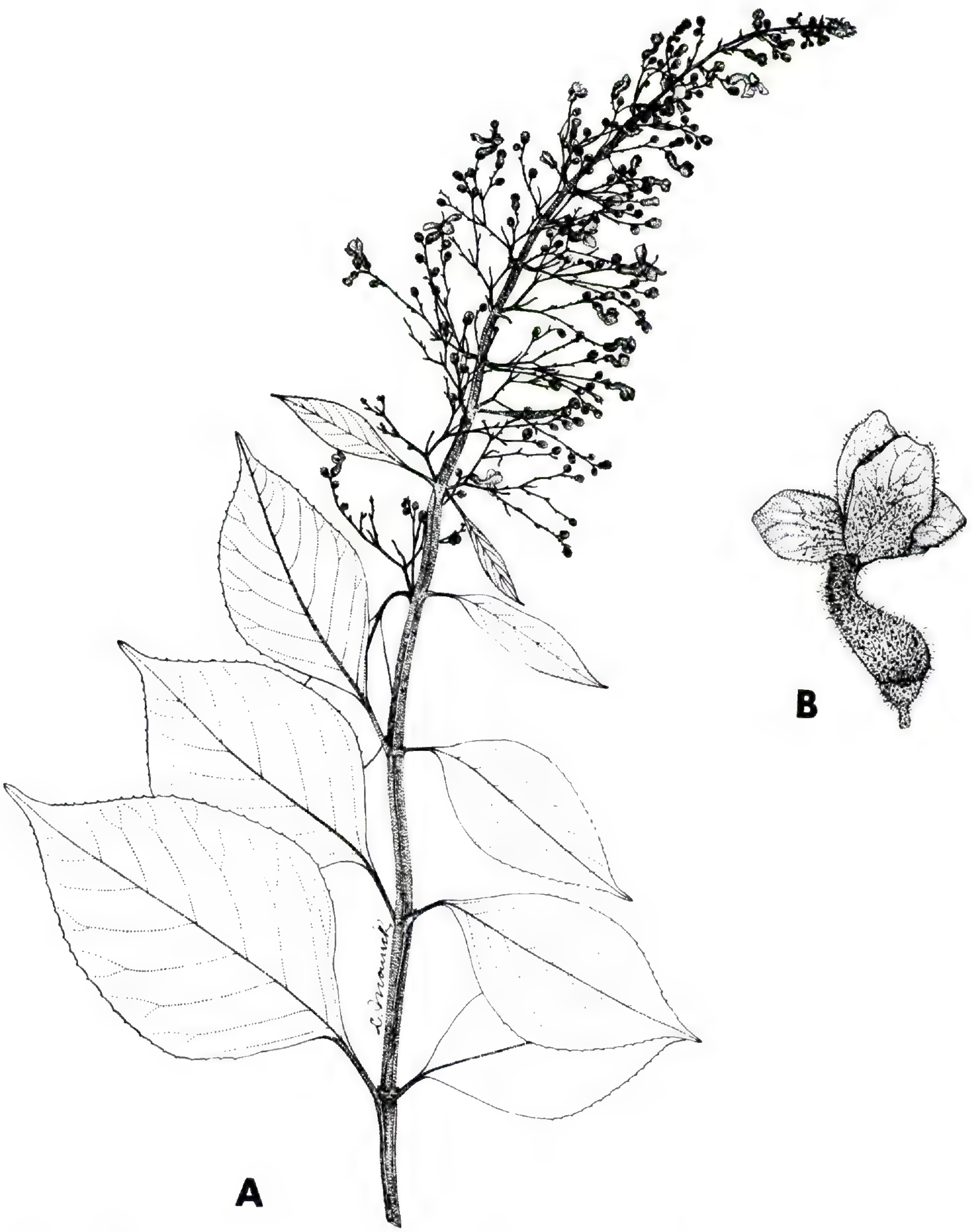

FIGURE 13. *Cornutia grandifolia* var. *normalis* (Kuntze) Moldenke—A. Habit with inflorescence (× ⅜).—B. Flower (× 3). [After *Duke 5680* (Mo).]

lets, petioles, leaf-blades, peduncles, sympodia, and inflorescence-branches being much shorter and more appressed and the young flower-buds being conspicuously hirsute with long, spreading hairs.

Thickets and open scrub, forested riverbanks, wet savannas, pastures, roadsides, and waste places, Costa Rica and Panama. It is occasionally cultivated elsewhere.

BOCAS DEL TORO: *Dunlap 575* (F, US). CANAL ZONE: 1931, *Bailey & Bailey 551* (F, PNH). Near USARSO chemical training camp area, *Correa & Stimson 19* (MO, NY). Albrook, *Dwyer 1073* (MO). Cutover second growth, Naval Reservation, *Ebinger 485* (MO). Matachin, *Kuntze 1932* (MO-type collection). Roads and waste places around Gamboa, *Pittier 3702* (US). Western slope of Ancon Hill, *Seibert 113* (MO). Miraflores Locks, *Stern et al. 56* (MO, MOLDENKE). Near Survival School, Curundu, *Tyson 1060* (MO). Miraflores Locks area, *Tyson 1260* (MO). Fort Clayton, Cardenas Creek area, *Tyson 1274* (MO). Howard Air Force Base near Red Devil drop zone, *Tyson 1874a* (MO). Without locality, *Bartlett & Lasser 16528* (MICH); *Bro. Gervasius 112* (US); *Maxon & Harvey 6610* (US); *Pittier 6711* (US); *Standley 25471* (US). CHIRIQUÍ: Pastures and forested riverbanks E of Gualaca, 500 ft, *Allen 5034* (MO). Tolé, near Santa Ana Well, 1000 ft, *Dwyer & Kirkbride 7462* (MO, US). Highway between Río Tabasara and Río Tinta, *Woodson et al. 412* (MO, NY, US). Without locality, *Cooper & Slater 225* (F, US, YU); *Wagner s.n.* (M). COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1637, 1795* (both NY, US). Between Las Margaritas and El Valle, *Woodson et al. 1737* (MO, NY, US). LOS SANTOS: 1–2 mi. W of Candelaria, *Duke 12446* (MO). 10.8 mi. S of Macaracas, *Lewis et al. 1620* (NY, US). PANAMÁ: Pearl Islands, *Anderson*, 1852 (S). Panamá, *Bartlett & Lasser 16529* (MICH). Chepo, *Dodge s.n.* (F). Gallery along Rio Mamoni, *Duke 5680* (MO). Open scrub near Balf Hill, San Jose Island, *Erlanson 311* (DS, MICH, NY). Panamá, *Hayes s.n.* (E); *Maxon & Harvey 6661* (US). Sabanas N of Panamá City, *Bro. Paul 473* (MICH, NY, US). Laguna de Portala, Chepo, 60 m, *Pittier 4617* (GH, NY, US). Between Río Pacora and Chepo, roadside savanna, *Porter et al. 5152* (MEOW). Savannas, *Riley 120* (BM, K, MO, US). Panamá, *Seemann 257* (BM-in part). Panamá, *Stevens 610* (ILL). Wet savannas E of Pacora, 25 m, *Woodson, Allen & Seibert 758* (MO, NY). Río Tatare, *Woodson & Schery 1002* (MO, NY, US). VERAGUAS: Roadside savanna 2–4 mi. E of Santiago, 30 m, *Duke 12364* (MO).

2. **Cornutia microcalycina** Pavon *ex* Moldenke, Feddes Repert. 40: 173–174. 1936.

Shrub or small *tree* to 5 m tall; branches stout, obtusely or acutely tetragonal, medullose or hollow, often deeply 4-sulcate in drying, sometimes margined or alate, densely puberulent; nodes decussately flattened, occasionally somewhat swollen, distinctly and often prominently annulate. *Leaves* membranous or chartaceous, broadly elliptic, 17.5–27 cm long and 7.8–14 cm wide entire, apically acuminate, basally acute or acuminate, dark-green above, lighter beneath, strigillose-puberulent or densely pubescent above, densely cinereous-tomentose beneath, petioles stout, 2.5–6 cm long, densely puberulent or short-pubescent, flat above and often margined almost to the base. *Inflorescences* terminal, thyrsoid, 22–38 cm long and 7–10 cm wide, many-flowered, of cymes in 6–9 pairs and one apical, occasionally also 1–2 pairs of small cymes in the uppermost axils, densely puberulent throughout, the cymes several times dichotomous; peduncle (3–7 cm long) and sympodia similar to the branchlets but more slender; few foliaceous bracts sometimes present, long-stipitate, resembling the uppermost leaves but smaller; bractlets linear, 2–4 mm long densely puberulent; prophylls minute, setaceous, densely puberulent. *Flowers* with the calyx cupuliform or patelliform, ca. 1 mm long and 1.5 mm wide, densely short-pubescent, with teeth 0.1 mm long, obscured by the pubescence, corolla hypocrateriform, densely short-pubescent outside and inside, the tube slightly curved, the adaxial side ca. 10.1 mm, the abaxial side ca. 8.3 mm long, ca. 3.1 mm wide apically, the abaxial lobe oblong-lingulate, ca. 5.2 mm long and wide, obtuse, the adaxial lobes broadly elliptic-lingulate, ca. 3.1 mm long and 3.6 mm wide, rounded; ovary ca. 1 mm long and wide, densely long-hirsute.

Coastal plains and forests, open fields or thickets, from Panama to Peru.

DARIÉN: Open field at old town of Cana, 1750 ft, *Stern et al. 471* (MO, MOLDENKE).

2a. **Cornutia microcalycina** var. **anomala** Moldenke, Feddes Repert. 40: 176. 1936.

This variety differs from the typical variety in the pubescence on the upper and lower leaf-surfaces being long-pubescent, long-pilose, or villous with long, white, glistening, multicellular hairs strigosely appressed above and subtomentose beneath. The branches and branchlets are glabrescent.

Cliffsides and banks of streams, Panama, Colombia, and Cocos Island.

DARIÉN: Near Cana, 600 m, *Goldman 1896* (US).

2b. **Cornutia microcalycina** var. **pulverulenta** Moldenke, Feddes Repert. 40: 175. 1936.

This variety differs from the typical variety in the lower leaf-surfaces being densely pulverulent-puberulent.

Mostly in humid tropical forests from Panama to Ecuador.

CANAL ZONE: *Johansen 41* (US). COCLÉ: Boca del Toabré at confluence of Río Toabré and Río Cocle del Norte, *Lewis et al. 5502* (MOLDENKE). DARIÉN: Between Cañasas and Sabalo, 100 m, *Duke 14454* (MO). Above tide limit, Sambú River, *Pittier 5690* (BM, GH, NY, US).

14. VITEX

Vitex L., Sp. Pl. 635. 1753; Gen. Pl., ed. 5. 285. 1754.

Mailelou Rheede *ex* Adans., Fam. Pl. 2: 12, 200. 1763.
Limia Vand., Fl. Lusit. 42, *pl. 3, fig. 21.* 1788.
Nephrandra Willd. *in* Cothen., Disp. Veg. 8. 1790.
Allasia Lour., Fl. Cochinch., ed. 1. 84. 1790.
Tripinna Lour., Fl. Cochinch. ed. 1. 476. 1790.
Chrysomallum Thou., Gen. Nov. Madag. 8. 1806.
Tripinnaria Pers., Syn. Pl. 2: 173. 1806.
Pyrostoma G. F. W. Mey., Prim. Fl. Esseq. 219. 1818.
Wallrothia Roth, Nov. Pl. Sp. 317. 1821.
Ephialis Banks & Soland. *ex* A. Cunn., Ann. Nat. Hist., Ser. 1. 1: 461. 1838.
Psilogyne A. DC., Biblioth. Universelle Genève 17: 132. 1838.
Casarettoa Walp., Repert. 4: 91. 1844.
Macrostegia Nees *in* DC., Prodr. 11: 218. 1847.
Agnus-castus Carr., Rev. Hort. 42: 415. 1871.
Varengevillea Baill., Hist. Pl. 11: 116, in part-flowers only. 1892.

Trees or *shrubs*, rarely woody vines, glabrous, tomentose or villous. *Leaves* decussate-opposite or ternate, palmately 3–7 foliolate, rarely 1-foliolate, the leaflets chartaceous or membranous, sometimes coriaceous, mostly petiolulate, entire or dentate, rarely incised or lobed. *Inflorescences* cymose, the cymes short and dense or loosely divaricate, sessile or pedunculate in the leaf-axils or aggregated in terminal racemiform, thyrsoid or laxly diffuse panicles, more rarely contracted into heads, occasionally few- or 1-flowered, rarely cauliflorous; flowers perfect, more or less zygomorphic; bractlets and prophylls usually very small, mostly linear, sometimes longer than the calyx. *Flowers* with the calyx campanulate, cyathiform, or rarely tubular-infundibular, 5-dentate, or 5-fid, rarely 3-fid or 6-lobed, the teeth mostly slightly unequal; corolla white, blue, violet or yellowish, long-tubular,

cylindric, or hypocrateriform, zygomorphic, the tube short or rarely elongate, cylindric, straight or slightly incurved, sometimes slightly ampliate above, the limb oblique, spreading, more or less bilabiate, the upper lip often bifid, the lower lip trifid, the two posterior lobes exterior and usually shorter, the lateral lobes larger, the anterior lobe largest, entire or emarginate, the upper lip erect, arched, or resupinate; stamens 4, didynamous, inserted in the corolla-tube, often exserted, the anthers 2-celled, the thecae distinct, parallel to divergent or arcuate, attached near the apex, dehiscing by longitudinal slits; pistil single, compound, bicarpellate, the style terminal, filiform, shortly bifid apically, the branches acute, the ovary at first imperfectly 2-celled, during anthesis usually 4-celled, the cells 1-ovulate; ovules attached laterally at or above the middle of the cell. *Fruit* drupaceous, fleshy, the endocarp hard, often horny, sometimes incrassate in relation to the cells, 4-celled; seeds obovate or oblong, erect, without endosperm; fruiting-calyx often accrescent, usually patelliform or very shallowly cupuliform, rarely partly enclosing the fruit.

A complex genus of about 380 specific and infraspecific entities, mostly of the tropics and subtropics of both hemispheres, a few also found in temperate Europe and Asia. Species are widely cultivated and naturalized. A few fossil forms are known from Europe and Africa. The African genus *Chrysomallum*, listed in the synonymy above, may be worthy as a separate genus.

a. Inflorescence paniculate or thyrsoid.
  b. Leaves 3-foliolate, glabrous or glabrate beneath, smooth above; introduced ---------- 1. *V. parviflora*
  bb. Leaves 3–5 foliolate, densely tomentose beneath, mostly subbullate-rugose above, native ---------- 2. *V. masoniana*
aa. Inflorescence cymose.
  c. Leaves 3-foliolate.
    d. Lateral leaflets usually much smaller than the central one ---------- 3. *V. cooperi*
    dd. Lateral leaflets usually not much smaller than the central one ---------- 4. *V. floridula*
  cc. Leaves 3–7 foliolate.
    e. Leaflets densely and softly short-pubescent or velutinous-tomentellous beneath ---------- 5. *V. flavens*
    ee. Leaflets becoming sparsely short-pubescent or puberulent beneath when mature ---------- 6. *V. cymosa*

1. **Vitex parviflora** A. L. Juss., Ann. Mus. Natl. Hist. Nat. 7: 76. 1806.

V. littoralis Decne., Nouv. Ann. Mus. Hist. Nat. 3: 401. 1834, non *V. littoralis* A. Cunn., Ann. Nat. Hist., Ser. 1. 1: 461. 1838.
V. altissima Blanco, Fl. Filip., ed. 1. 516. 1837, non *V. altissima* L. f., Suppl. Pl. 293. 1781.
V. glaberrima Zipp. *ex* Span., Linnaea 15: 330. 1841.
V. timoriensis Walp., Repert. Syst. 4: 84. 1844.
V. leucoxylon Span. *ex* Miq., Fl. Ind. Bat. 2: 863. 1856, non *V. leucoxylon* L. f., Suppl. Pl. 293–294. 1781.
V. cofassus var. *timorensis* H. Hallier, Meded. Rijks-Herb. 37: 47. 1918.
V. glandulosa H. J. Lam, Verbenac. Malay. Archipel. 199. 1919.

Often much gnarled *tree* to 17 m tall, trunk to 90 cm d.b.h., branched from below the middle; branchlets mostly ampliate and thickened at the nodes, obtusely tetragonal, gray, lenticellate, glabrous; twigs buff or brownish, usually conspicuously white-lenticellate, minutely puberulent with short canescent or brownish hairs, glabrescent. *Leaves* 3-foliolate; leaflets subequal or the lateral 2 slightly

smaller, leaflets chartaceous, mostly drying uniformly grayish-green on both surfaces, the central one oblong-elliptic or elliptic, 4–17.5 cm long and 2.2–7 cm wide, apically acuminate or caudate, varying to acute or even obtuse on smaller leaflets, entire or wavy-margined, abruptly acute or short-acuminate basally, minutely and obscurely puberulent on both surfaces or glabrous and shiny, the lateral pair similar but apically less caudate; petioles 3–7.5 cm long, sparsely and minutely pulverulent-puberulent, glabrescent; petiolules 3–19 mm long, slender, conspicuously canaliculate and minutely pulverulent or glabrate. *Inflorescences* axillary and terminal, paniculate-thyrsoid, erect or ascending, pinkish-gray, 10–21 cm long and 4.5–13.5 cm wide, often with 1–5 opposite pairs of paniculate branches, sometimes simple, each panicle of 4–10 or more pairs of stipitate, flowered cymes; peduncles 2–4 cm long, the rachis and inflorescence-branches slender, similar to the twigs in texture, color and puberulence or sometimes densely canescent-puberulent; pedicels mostly obsolete; foliaceous bracts often present in the larger thyrsoid inflorescence, 2–3-foliolate, long-stipitate, similar to the leaves but much smaller; bractlets and prophylls linear, 1–3 mm long or less, caducous. *Flowers* with the corolla blue or light-blue to purplish-blue or purple. *Fruit* black, ca. 8 mm wide.

Steep slopes, rocky headlands, grassy slopes, and thickets near the sea throughout the Philippine Islands and Indonesia. The species is widely cultivated in subtropical and tropical lands, introduced in Panama for its wood which was used for railroad ties.

In its native range the inflorescence is often partly or wholly replaced by great masses of tomentose bracts, bracteoles and galled flower-buds caused by the action of a *Cecidomya* insect.

BOCAS DEL TORO: Cultivated, Almirante, Farm Number 5, Changuinola District, *Seibert 1535* (MO).

2. **Vitex masoniana** Pittier, Contr. U. S. Natl. Herb. 18: 170. 1916.—FIG. 14.

Tree, to 50 m tall, the trunk to 95 cm d.b.h.; branchlets stout and acutely tetragonal, mostly sulcate between the angles, densely furfuraceous-puberulent or short-pubescent with brownish hairs, somewhat lenticellate, glabrescent; twigs more densely brown-furfuraceous, often compressed. *Leaves* 3–5-foliolate, fully expanded at time of anthesis; leaflets subequal or the lowermost somewhat smaller, subcoriaceous, the central leaflet elliptic, 4.3–24.5 cm long and 1.8–10.3 cm wide, entire, apically acute or obtuse, often subrevolute along the margins, basally acute, light-green on both surfaces, glabrous and often subbullate-rugose above, densely short-pubescent beneath, the lateral leaflets similar but usually smaller, the vein reticulation usually impressed above and sharply prominent beneath, petioles 2–8.5 cm long, densely brown-furfuraceous; stout furfuraceous, margined petiolules 1–9 mm long. *Inflorescences* axillary, paniculate, 6.5–18.5 cm

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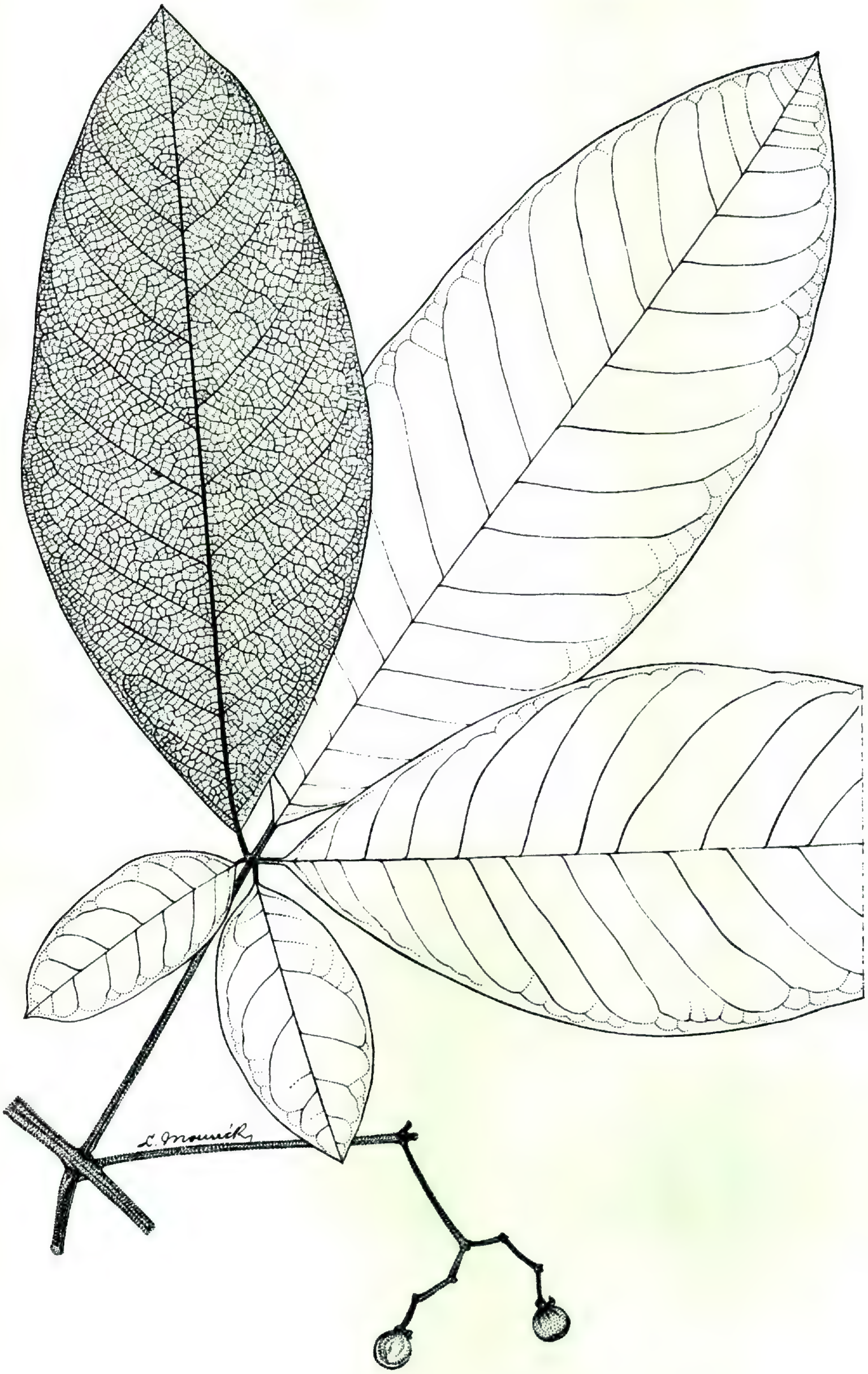
FIGURE 14. *Vitex masoniana* Pittier, habit with fruits (× ½). [After *Tyson et al. 4847* (MO).]



long and 3.5–6.5 cm wide, of 2–5 opposite pairs of long-stipitate, many-flowered cymes and a terminal cyme, furfuraceous-puberulent with brownish hairs throughout; peduncles 3.5–5.5 cm long, flattened; pedicels ca. 1 mm long or obsolete; foliaceous bracts often present, 3-foliolate, stipitate, to 3.5 cm long and 3 cm wide, the segments resembling ordinary leaflets but smaller; bractlets linear or oblong, 2–6 mm long; prophylls linear, 1–2 mm long; corolla blue to lavender or pale-purple, the central lobe of the lower lip usually purple, yellow in the throat, the other lobes lavender to even white; filaments white; anthers black. *Flowers* with the calyx campanulate, ca. 3 mm long, densely ochraceous-puberulent or furfuraceous, resinous-glandular, very distinctly 5-lobed, the lobes narrowly lanceolate, ca. 1 mm long, erect or recurved-spreading. *Fruit* globose, brown, 1.3–1.5 cm long and wide, densely brown-furfuraceous or puberulent; fruiting-calyx patelliform, irregularly split, to 1 cm wide, densely brown-puberulent.

In forests and along roadsides, widely distributed but usually not numerous, Panama and Colombia.

DARIÉN: Trail between Pinogana and Yavisa, 15 m, *Allen 265* (MO, NY, US). Infrequent, near Yavisa, 100 ft, Río Chico, *Allen 4588* (MO, NY, S, US). Santa Fé, *Duke 8387* (LL, US). Between Río Punusa and Río Pucro, *Duke 14639* (AAU, MO). Trail to Río Pirre, near El Real, Río Tuira, *Stern et al. 299* (BM, MO). Near Campamento Buena Vista, Río Chucunaqua above the Río Tuquesa, *Stern et al. 903* (BM, MO). Near Campamento Buena Vista, Río Chucunaqua above the confluence with Río Tuquesa near Quebrada Félix, *Stern et al. 958* (BM, MO). Without locality, *Duke 13116* (AAU). PANAMÁ: Between Cañasas and Sabalo, *Duke 14489* (MO); *Klugge 44* (F, K, MOLDENKE, NY, PH, US, YU). Forests of the upper Mamoni River, 150–400 m, *Pittier 4489* (BM, GH, NY, PH, US).

3. **Vitex cooperi** Standl., Trop. Woods 16: 26, 29, 32, nom. nud. 1928; Publ. Field Columbian Mus., Bot. Ser. 4: 256. 1929.

Tree to 26 m tall; trunk buttressed and fluted, to 75 cm d.b.h.; wood durable; bark thin; branchlets acutely tetragonal varying to terete or compressed, grayish or brunneous, glabrescent densely fulvous puberulent when young. *Leaves* 3-foliolate; leaflets unequal in size, the lateral pair much smaller, thin-chartaceous or submembranous, the central leaflet broadly elliptic, 4.5–22 cm long and 2.5–10.5 cm wide, entire, apically rounded and short-acuminate or abruptly acuminate, the tip obtuse and apiculate, basally acute to acuminate, dark- or bright-green above, lighter beneath, shiny, glabrous above, finely puberulent beneath when young, especially on the larger venation, glabrescent, the lateral leaflets similar but smaller and narrower, petioles 1.3–9.5 cm long, finely appressed-puberulent, petiolules 1–8 mm long, the central one longest, stout, finely puberulent, flattened, and decidedly margined. *Inflorescences* axillary, solitary, cymose, blooming after the leaves have matured, 3.5–14 cm long and 4–6 cm wide, ca. 4 times dichotomously branched, many-flowered, usually loose and divergent, finely puberulent throughout; peduncles conspicuously flattened, 4.5–7.5 cm long; pedicels slender, 1–3 mm long; foliaceous bracts few, ca. 1.5 cm long and 4 mm wide, simple, long-stipitate; bractlets and prophylls linear, 1–3 mm long. *Flowers* fragrant, corolla blue or lavender.

In wet thickets from sea level to 600 m, said to be fairly common on hilly land bordering Gatun Lake on the Atlantic watershed. *Vitex cooperi* occurs from Guatemala to Panama.

The wood is durable on contact with soil, splits easily in straight lines, and is used for implement handles, posts, cross-ties, and stringers, as well as in house construction. The wood seems to have a perishable heart, because one often finds trees standing with the trunk in a shell-like state. Insects and other animals inhabit the inner hollow. Samples of the wood have been made into beautiful turnery and canes, as well as table-top inlays. It works up under plane and knife much like teak. It often has a beautiful streaked or mottled figure. The name "yellow manwood," used by Panamanian and Costa Rican negroes, refers to its strength and durability. The wood is sometimes confused with "black manwood" (*Minquartia guianensis*).

CANAL ZONE: Azote de Caballo road near Madden Dam before first saddle dam, *Stern & Chambers 159* (MO, NY, US). CHIRIQUÍ: Progreso, *Cooper & Slater 156* (AAH, F, GH, NY, PH, US, YU), *195* (F, GH, NY, US, YU), *241* (F, NY, US, YU). Near San Felix, 0–120 m, *Pittier 5267* (GH NY, US). Near San Bartolomé, Peninsula de Burica, 0–50 m, *Woodson & Schery 937* (MO, NY, US). Without locality, *Duke 13572* (BMIC). VERAGUAS: *Fischer 1* (F, YU).

4. **Vitex floridula** Duchass. & Walp. *in* Walp., Ann. Bot. Syst. 3: 240. 1852.

Tree to 20 m tall; trunk rough, shaggy; wood very hard; crown low, rounded; branches and branchlets light-gray or whitish, obtusely tetragonal, minutely puberulent, glabrescent, corky, densely lenticellate, more densely gray-puberulent on the younger parts. *Leaves* 3-foliolate, developing after the flowers; leaflets firmly chartaceous and thick when mature, elliptic, 4–14.8 cm long and 2.2–8 cm wide, apically acute or short-acuminate, entire, usually subrevolute along the margins when mature, shiny on both surfaces, dark-green above, bright-green beneath, glabrate on both surfaces, the lateral pair similar to the central leaflet but smaller; petioles 2.5–7 cm long, minutely and obscurely puberulent or glabrate; petiolules 5–11 mm long, minutely puberulent, the central petiolule longer than the lateral pair. *Inflorescences* axillary, developed before the leaves. *Flowers* with the corolla purple or light-violet.

In forests on dry limestone soil and along rivers at low elevations, apparently endemic to Panama.

CANAL ZONE: Summit, *Haynes 464* (NY, NY). Hospital grounds at Ancón, *Mason 10* (US). West side of canal near island, *White 89* (NY). Without locality, *Christopherson 153* (US); *Hayes 15* (E); *Hayes s.n.* (K); *Jones 325* (US). DARIÉN: Forests around Yaviza, *Pittier 6585* (NY). Near La Palma, 0–50 m, *Pittier 6604* (US). Forests around Pinogana, *Pittier 6626* (NY). PANAMÁ: Along Río Chagres between Gamboa and Alajuela, 30–60 m, *Allen 959* (DS, MICH, MO, NY, S, UC, US). Panamá, *Duke & Bristan 8258* (BMIC). Forests on dry limestone around Alajuela, Chagres Valley, 30–100 m, *Pittier 3477* (AAH, BM, CP, F, GH, K, NY, US). Sabana de Juan Corso near Chepo, 60–80 m, *Pittier 4683* (GH, NY, US). Panamá, *Pittier 6585* (NY, US), *6604* (F, GH, MO, US), *6626* (BM, GH, NY, US).

5. **Vitex flavens** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 199. 1817.

V. *rusbyi* Moldenke, Phytologia 1: 103. 1934.

Shrub or *tree* to 20 m tall; branchlets stout, obtusely tetragonal, gray or brownish, flavescent-tomentose when young, becoming merely brown-puberulent or even glabrescent, not noticeably lenticellate, the twigs densely short-pubescent with flavescent or fulvous hairs. *Leaves* 5-foliolate, very immature at time of anthesis; membranous, the central leaflets oblong or lanceolate-oblong to narrow-

elliptic, 4–10 cm long and 1.5–3.7 cm wide, apically acute or short-acuminate, rarely obtuse, basally acute, entire, dark-green above, brunnescent or nigrescent in drying, flavescent or fulvous beneath, lightly appressed-pubescent throughout above, densely and softly velutinous-tomentellous beneath with flavescent or fulvous hairs, the lateral leaflets similar but often smaller and less acuminate; petioles 2–12 cm long, densely short-pubescent with flavescent or fulvous hairs; leaflets subequal or the lowermost pair somewhat smaller than the central leaflets, sessile or subsessile when immature but the petiolules becoming 2–12 mm long, densely flavescent or fulvous, short-pubescent or velutinous-tomentellous. *Inflorescences* axillary, cymose, 3–8 cm long and 1.5–4.5 cm wide, usually half as long as the subtending petiole, often corymbiform, 1–4 times dichotomous, usually densely many-flowered, canescent- or flavescent-puberulent or short pubescent throughout; peduncles 0.7–4.5 cm long, flattened; pedicels obsolete on lateral flowers or to 6 mm long on central flowers; bractlets oblong or spatulate to linear, sessile, 3–6 mm long; prophylls linear or setaceous, ca. 1 mm long. *Flowers* with the calyx campanulate, 2–3.5 mm long and wide, densely appressed-pubescent with short, flavescent, antrorse hairs, deeply 5-dentate, the teeth ovate-triangular, acute or blunt, often recurved or reflexed, brunnescent on the inner surface; corolla purple or lilac to blue, lavender-blue, or blue-violet, hypocrateriform the tube ca. 5 mm long, densely short-pubescent outside, the limb with 4 small lobes, 2–3 mm long, obtuse, the lower lip greatly enlarged, lingulate, 6–7 mm long, crisped along the rounded margins. *Fruits* fleshy drupes ca. 5 mm long and wide; fruiting-calyx cupuliform, ca. 4 mm long and 5 mm wide, triangular-toothed.

Apparently widespread from Colombia to Ecuador, Peru, and Amazonian Brazil; on hilly land, light forests, especially rocky hills, bluffs, gorges, damp ground in quebradas, and streamsides.

In Ecuador the wood is considered excellent for building houses.

"Taruman," "taruman tuira," "acietuno," "pechiche," "taruma," "mameira," "tarumá grande do campo."

I have seen no Panama material, but there is a collection, *Barclay s.n.* (K) labeled "Central America." The Pavon specimens labeled "Nueva Espana" are probably from Peru.

6. **Vitex cymosa** Bert. *ex* Spreng. *in* L., Syst. Veg. ed. 16. 2: 757. 1825.

Jatropha tomentosa Spreng. *in* L., Syst. Veg., ed. 16. 3: 77. 1826.
Vitex discolor Glaz., Bull. Soc. Bot. France, Mém. 3: 547. 1911.
V. cujabensis Mart. *ex* Benth., Bot. Voy. Sulphur 155. 1846.

Tree to 28 m tall; trunk to 60 cm in diameter 1.5 m above ground; branchlets gray to brownish, acutely or obtusely tetragonal, the pith small, the youngest parts densely puberulent with sordid-grayish or yellowish hairs. *Leaves* 3–7-foliolate, sometimes subopposite; leaflets usually unequal in size, the two lowermost usually considerably smaller, the central leaflet oblong or elliptic to oblanceolate-elliptic or obovate, rarely lanceoate, 4–23 cm long and 2.4–7.2 cm wide, apically acute to abruptly short-acuminate or even caudate-acuminate, the acumen itself blunt, basally acute or acuminate-attenuate, entire, green on both surfaces when mature or lighter beneath, brunnescent or nigrescent above when immature,

firmly chartaceous or rarely subcoriaceous when mature, very lightly and obscurely pulverulent-puberulent above when immature, usually glabrescent and shiny when mature, puberulent to short-tomentellous (sometimes very densely so) beneath when immature, less so when mature; petioles 2.5–15 cm long, densely puberulent or short-pubescent; petiolules 1–17 mm long when mature, densely puberulent, margined, the lateral petiolules usually shorter than the central ones, often obsolete on immature leaves. *Inflorescences* axillary, cymose, abundant, much shorter than the subtending petioles, 2–9.5 cm long and 1–10 cm wide, 1–4 times dichotomous with wide-spreading branches, usually flowering before the leaves are completely mature, whitish- or yellowish-puberulent throughout, the hairs denser at all the joints; peduncles 0.7–4.5 cm long, the cyme-branches conspicuously flattened; pedicels 1–2 mm long; foliaceous bracts often present, simple, obovate-spatulate or oblong-elliptic, stipitate 1–1.5 cm long, similar to the immature leaflets in pubescence; bractlets linear, 1–4 mm long; prophylls setaceous, ca. 1 mm long. *Flowers* with the calyx campanulate, 2–3 mm long and 2–5 mm wide, densely puberulent, 5-dentate, the teeth ovate, obtuse or acute, often recurved or reflexed, often nigrescent on the inner surface; corolla blue or pinkish-blue to violet, lilac, or purple, rarely white, hypocrateriform, the tube 6–7 mm long, puberulent outside above the calyx, the limb conspicuously 2-lipped, the 4 small lobes ca. 4 mm long and 2 mm wide, obtuse, the fifth lobe much enlarged, rounded, ca. 7 mm long and 8 mm wide, the margins crisped. *Fruit* succulent, purplish- or violet-black, 1.1–2 cm long and 0.9–1.5 cm wide, glabrous, edible; fruiting cymes usually 4–6.5 cm long and lax, the pedicels 1–5 mm long, strigose-pubescent; fruiting-calyx flattened-campanulate, ca. 5 mm long and 12 mm wide, shallow, coriaceous, dark, finely short-strigose outside, 4- or 5-lobed, the lobes broadly triangular-ovate and often more or less obscurely toothed.

A variable species ranging from Panama to Bolivia, Paraguay, and northern Argentina. It grows on both high ground and on inundated land, in thickets, the margins of woods, open woods and virgin forests, savannas, arid coastal areas, and cactus deserts.

The fruits are edible, very sweet with a peculiar after-taste.

"Azietuno," "cañaguate," "cuajado," "tarumá," "tarumá do igapó," "tarumá do alagado," "jaramantaia," "tarumá de varzea."

DARIÉN: Río Pirre, "cuajado," *Duke & Bristan 8244* (MO).

15. CLERODENDRUM

Clerodendrum L., Sp. Pl. 637. 1753; Gen. Pl., ed. 5. 285. 1754.

Siphonanthus L., Sp. Pl. 109. 1753; Gen. Pl., ed. 5. 47. 1754.
Ovieda L., Sp. Pl. 637. 1753; Gen. Pl., ed. 5. 284. 1754.
Volkameria L., Sp. Pl. 637. 1753; Gen. Pl., ed. 5. 284. 1754.
Montalbania Neck., Elem. 1: 273. 1790.
Volkmannia Jacq., Hort. Schoenbr. 3: 48, *pl.* 338. 1798.
Agricolaea Schrank, Denkschr. Königl. Akad. Wiss. München 98. 1808.
Torreya Spreng., Neue Endeck. 2: 221. 1821, non *Torreya* Raf., Amer. Monthly Mag. & Crit. Rev. 356. 1818, nec Raf., Jour. Phys. 89: 105. 1819, nec Arn., Ann. Nat. Hist., Ser. 1. 1: 130. 1838, non Croom *ex* Mesin., Gen. Comm. 34. 1843.
Egena Raf., Fl. Tellur. 2: 85. 1837.
Cornacchinia Savi, Mem. Mat. Fis. Soc. Ital. Sci. Modena, Pt. Mem. Fis. 21: 184, *pl.* 7. 1837.

Rotheca Raf., Fl. Tellur. 4: 69. 1838.
Clerodendron R. Br. *ex* Meisn., Gen. Pl. 1: 637. 1838.
Cyclonema Hochst., Flora 25: 225. 1842.
Spironema Hochst., Flora 25: 226. 1842, nec *Spironema* Raf., Fl. Tellur. 4: 92. 1836, non Lindl., Bot. Reg. 26: *pl. 46*. 1840.
Cyrtostemma Kunze, Bot. Zeit. 1: 272. 1843.

Woody plants, mostly *trees* or *shrubs*, sometimes woody vines, usually unarmed or rarely with the petiole-base spinescent, glabrous or variously pubescent. *Leaves* simple, decussate-opposite or whorled, entire or variously dentate, deciduous, exstipulate. *Inflorescences* cymose, the cymes mostly loose-flowered, pedunculate in the upper leaf-axils, paniculate at the apex of the branchlets or densely aggregate in terminal corymbs or heads, the flowers rarely solitary. *Flowers* zygomorphic, often large and showy, mostly white, blue, violet, or red, the calyx the same color as the corolla or contrastingly red, white, or green; calyx campanulate or rarely tubular, truncate, 5-toothed, or 5-fid, often accrescent, spreading and subtending the fruit or enclosing it; corolla hypocrateriform, gamopetalous, the tube narrowly cylindric, straight or incurved, sometimes slightly ampliate at the mouth, often elongate, more rarely only slightly exceeding the calyx, the limb spreading or subreflexed, 5-parted, the lobes subequal or the posterior and exterior pairs slightly shorter and the anterior one larger, sometimes concave; stamens 4, didynamous, inserted in the corolla-tube, long-exserted, involute in bud, perfect, alternate with the corolla-lobes, the anthers ovate or oblong, 2-celled with parallel thecae, opening by longitudinal slits; pistil one, compound, 2-carpellate, the style terminal, elongate, shortly and acutely 2-fid apically, the ovary imperfectly 4-celled, each cell 1-ovulate, the ovules high-lateral, hemianatropous. *Fruit* drupaceous, globose or obovoid, often 4-sulcate and sub-4-lobed, the exocarp more or less fleshy, the endocarp bony or crustaceous, smooth or variously rugose, separating on maturity into 4 pyrenes or these sometimes cohering in pairs; seeds oblong, without endosperm.

A complex genus of about 560 species and named varieties (largest genus in the family) of tropical and subtropical regions, most abundant in Asia and Africa, poorly represented in America except in cultivation and by naturalization. A few species extend into temperate zones. Six species of fossil forms are known from the Tertiary of Europe and Africa. *Cyclonema* may be worthy of segregation as a distinct genus.

a. Leaves large, coarsely dentate or deeply lobed.
  b. Leaf-blades deeply lobed, densely squamose beneath; inflorescence widely pyramidal-paniculate; corolla scarlet or deep-orange ..... 1. *C. paniculatum*
  bb. Leaf-blades irregularly coarse-dentate, not squamose beneath; inflorescence a short compact cyme; corolla white or pinkish ..... 2. *C. philippinum*
aa. Leaves smaller, entire.
  c. Corolla blood-red; calyx white during anthesis, purple or pink after anthesis, split to the base, the lobes ovate, large, foliaceous, to 2 cm long and 1 cm wide; vine; leaf-scars usually not sharply elevated ..... 4. *C. thomsonae*
  cc. Corolla white; calyx green, split only ½–¾ way to the base, the lobes narrowly lanceolate; shrubs; leaf-scars mostly much elevated and elongated, often sharp.
    d. Leaf-blades acuminate at the apex.
      e. Leaves ternate, puberulent beneath ..... 5a. *C. ligustrinum* var. *nicaraguense*
      ee. Leaves opposite, glabrous beneath ..... 5. *C. ligustrinum*
    dd. Leaf-blades rounded or obtuse at the apex, sometimes acute.

f. Leaf-blades tomentose or tomentellous beneath, to 3 cm wide ..... 6. *C. molle*
ff. Leaf-blades glabrous beneath, to 1 cm wide ..... 3. *C. pittieri*

1. **Clerodendrum paniculatum** L., Mant. 1: 90. 1767.—Fig. 15.

Volkameria angulata Lour., Fl. Cochinch., ed. 1. 2: 389. 1790.
Caprifolium paniculatum Noronha, Verh. Batav. Genootsch. Kunsten 5: 9. 1790.
Clerodendron diversifolium Vahl, Symb. Bot. 2: 75. 1791.
C. pyramidale Andr., Bot. Repos. 10: *pl.* 628. 1810.
C. splendidum Wall. *in* Griff., Notul. 4: 169. 1854.
Cleianthus coccineus Lour. *ex* Gomes, Mem. Acad. Ci. Lisboa, Cl. Sci. Mor. Pot. Bel.-Let., n.s. 4(1): 28. 1868.

Bushy *herb* or erect *shrub*, to 3 m tall, woody at the base; branchlets stout, medullose or hollow, obtusely tetragonal, usually deeply sulcate in drying, minutely pulverulent-puberulent or glabrate, the nodes with a broad band of tomentose hairs. *Leaves* opposite, gradually smaller upwards; ovate, 6–40 cm long and 7–38 cm wide, basally cordate (3–7-lobed, the uppermost often entire and basally hastate), the lobes triangular-ovate, acute or apiculate, spreading, variable in size, the margins remotely apiculate-denticulate to crenate-dentate or entire, thin-chartaceous or membranous, bright green and usually shiny above, lighter and dull beneath, pulverulent and minutely strigillose above or glabrate, densely squamulose with orbicular peltate scales and punctate beneath, glabrous between the scales or pubescent only on the venation, the central lobe mostly ovate, the others much smaller and triangular; petioles 1.2–3.5 cm long, minutely pulverulent-puberulent or glabrate. *Inflorescences* axillary cymes in the uppermost leaf-axils and terminal panicles, the cymes long-pedunculate, 9–13 cm long and 3–7 cm wide, many-flowered, panicles often large and thyrsoid, to 39 cm long and 26 cm wide, 1–4 times dichotomous, many-flowered, of 4–16 pairs of cymes, the ultimate divisions often racemiform, the branches divaricate-ascending, conspicuously bracteate, minutely pulverulent-puberulent or glabrate throughout but often tomentose at the sympodial nodes; peduncles 1.5–12 cm long; pedicels rose-color, almost filiform, 4–15 mm long; foliaceous bracts large, a pair subtending each of the larger pairs of inflorescence-branches, ovate-elliptic, entire or obscurely 3-lobed, similar to the leaves; bractlets and prophylls linear, 1–10 mm long, puberulent. *Flowers* slightly odorous, buds red; calyx red or orange-red, 3–5 mm long, short-pubescent, divided to near the base, the segments erect and spreading, corolla orange-red to scarlet, short-hairy, the tube 1.2–1.6 cm long, the lobes of the limb 7–8 mm long, separated in the throat by white streaks, the posterior pair shorter and narrower than the others; filaments exserted 2.5–3.5 cm. *Fruit* greenish-blue to black.

A spectacularly showy plant, native to southeastern Asia, Pacific islands where it inhabits evergreen jungles, open forests, thickets, open fields, railroad embankments, roadside hedgerows, clearings, and shrub vegetation. It is widely cultivated in tropical and subtropical regions and often naturalized.

"Scarlet glorybower," "danger-flower," "red pagoda-flower."

CANAL ZONE: Cultivated in yard, *Blum & Kimmel 2281* (MO). Barro Colorado Island, *Ebinger 40* (MICH, MO, US); *Tyson 4207* (MO).

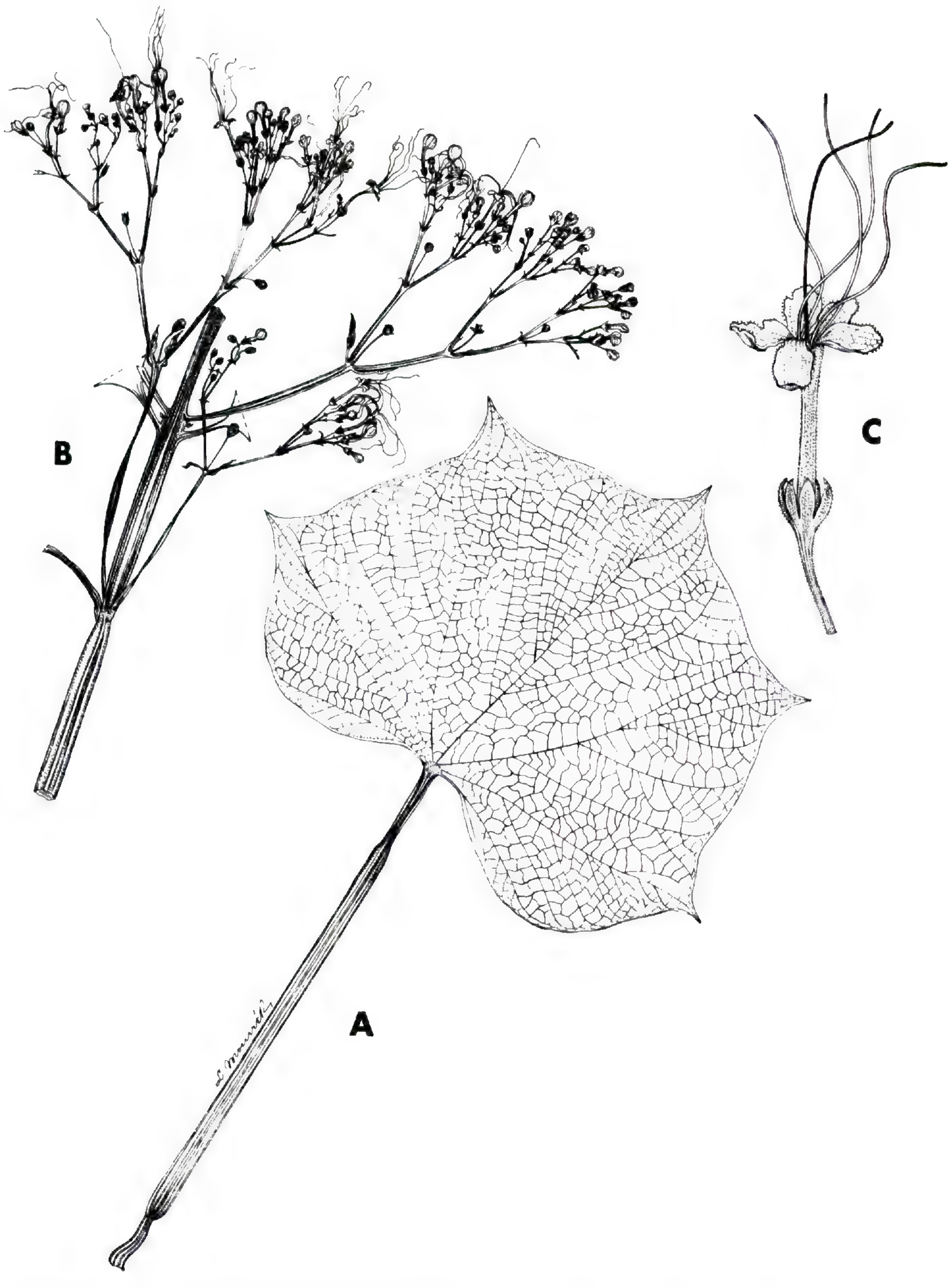


FIGURE 15. *Cleorodendrum paniculatum* L.—A. Leaf (× 3⅓).—B. Inflorescence (× 2⅓).—C. Flower (× 1⅔). [After *Blum & Kimmel 2281* (MO).]

2. **Clerodendrum philippinum** Schau. *in* DC., Prodr. 11: 667, as "*Clerodendron.*" 1847.

Volkmannia japonica Jacq., Hort. Schoenbr. 3: 48, *pl.* 338. 1798, non *Clerodendrum japonicum* (Thunb.) Sweet.
Volkameria fragrans Vent., Jard. 2: *pl. 70.* 1804.
Agricolaea fragrans Schrank, Denkschr. Königl. Akad. Wiss. München 98. 1808.
Clerodendrum fragrans Willd., Enum. Hort. Berol. 659. 1809.
C. fragrans Ait., Hort. Kew. 4: 63. 1812.
C. fragrans var. *multiplex* Sweet, Hort. Brit. 322. 1827.
Clerodendron fragrans β pleniflora Schau. *in* DC., Prodr. 11: 666. 1847.
Ovieda fragrans (Willd.) A. S. Hitchc., Mem. Torrey Bot. Club 12: 63. 1902.
Viburnum deltoideum M. E. Jones, Extr. Contr. West. Bot. 18: 68. 1933.
Clerodendron fragrans var. *flore-pleno* Hort. *ex* Penna, Rodriguésia 2: 315. 1936.
Clerodendrum fragrans cv. *'Pleniflorum'* Encke, Parays Blumergärt., ed. 2. 447. 1960.
C. japonicum var. *pleniflorum* (Schau.) Maheshwari, Taxon 15: 43. 1966.

Subshrub, to 1.5 m tall, mostly reproducing vegetatively; branches stout and angled, finely pubescent, the younger portions more slender and more densely short-pubescent. *Leaves* opposite, large, membranous, very fragile in drying, broadly ovate, 6–29 cm long and 5–28 cm wide, apically sharply acute, the margins coarsely and irregularly dentate, basally cordate to subtruncate, usually slightly prolonged into the petiole, lightly strigillose-pubescent on both surfaces, usually more densely so on the venation beneath, not squamulose; petioles 2–23.5 cm long, more or less densely short-pubescent, mostly collapsing basally and apically in drying. *Inflorescences* terminal, cymose, densely many-flowered, subsessile or short-pedunculate, 3–6 cm long and 3.5–9 cm wide, often subtended by a pair of foliaceous, long-stipitate bracts; bractlets numerous, foliaceous, scattered throughout the cymes, oblong or elliptic, 1.5–3 cm long and 3–12 mm wide, apically subulate-acuminate, basally attenuate-acute, strigillose-pubescent on both surfaces, especially at the margins, long-stipitate. *Flowers* with the calyx campanulate, 1–1.5 cm long, purple or red, with scattered circular or elliptic glandular disks at the margin, sparsely strigillose-puberulent or glabrate, 5-cleft, the lobes lanceolate, 4–10 mm long, sharply acuminate; corolla white to pink or rose-color, hypocrateriform; the stamens and pistil mostly modified into supernumerary petals. *Fruit* rarely developed.

An asiatic plant widely cultivated in all subtropical and tropical regions and tending to escape rapidly. It is naturalized from the southern United States and Mexico through the West Indies and Central America to Argentina, and Chile.

BOCAS DEL TORO: Near Almirante Bay, *von Wedel 15* (MO). DARIÉN: Near La Palma, 0–50 m, *Pittier 6694* (NY). Near Marraganti, 10–200 ft, *Williams 651* (NY).

3. **Clerodendrum pittieri** Moldenke, Phytologia 1: 416–417. 1940.

Shrub to 3 m tall; branches twiggy, stiff; branchlets and twigs rather slender, light gray, minutely puberulent with greatly appressed hairs, subglabrescent in age, the twigs often short, stiff and sharp-pointed, the internodes mostly abbreviated. *Leaves* opposite or ternate; thin-chartaceous, narrowly elliptic, 0.6–2.4 cm long and 2.3–10 mm wide, apically rounded or obtuse, entire, basally acute or subcuneate, dark green and glabrous on both surfaces but densely punctate beneath; petioles slender, 1–5 mm long, obscurely pulverulent-puberulent or glabrate, often spinescent at the base. *Inflorescences* axillary; cymes abbreviated,

solitary in the upper leaf-axils, 1–3 flowered, to 5.5 cm long (including the mature flower), lax; peduncles slender, 8–14 mm long, minutely and obscurely puberulent with appressed hairs; pedicels slender, 5–8 mm long, subglabrate; bracts and bractlets none; prophylls few, linear-subulate, 1–2 mm long; calyx campanulate, ca. 3 mm long, minutely puberulent or glabrate, apically truncate; corolla white or pale-purple, hypocrateriform, the tube 2–2.5 cm long, glabrous, the limb with lobes 7–10 mm long, apically subacute, stamens exserted ca. 2 cm. *Fruit* small, obovate, obtuse.

On or near sandy salt flats and mangrove lagoons, Guatemala to Venezuela and Ecuador.

The spinescent leaf-scars indicate its relationship to species 5 and 6 in this treatment.

CHIRIQUÍ: On dry edge of mangrove formation, El Pedregal de David, *Pittier 3374* (F, NY, US). COCLÉ: Along tidal belt and in savannas near sea level, Aguadulce, *Pittier 4965* (F, US). PANAMÁ: Panamá, *Seemann 1107* (BM, NY). Margin of mangrove swamp near Bejuco, *Dodge et al. 16729* (MO).

4. **Clerodendrum thomsonae** Balf. f., Edinburgh New Philos. Jour., Ser. 2. 15: 233, as "*Clerodendron*." 1862.

Clerodendron thomsoniae var. *balfourii* Jackson *ex* Dombrain, Fl. Mag. (London) 4: *pl. 255.* 1865.
C. balfourii Dombrain, Fl. Mag. (London) 4: *pl. 432*, in nota. 1869.
C. balfourianum Massart *et al.*, Mission Biol. Belg. Brésil 1922–23. 1: *fig. 52.* 1929.

High-climbing herbaceous or woody *vine* to 7 m long, more rarely a low shrub, 2–2.5 m tall; branchlets grayish, obtusely tetragonal, slender glabrate; twigs purplish or brown, densely puberulent; leaf-scars often large and circular, borne on prominent corky sterigmata, not spinescent. *Leaves* opposite; thin-chartaceous or membranous, often drying dark, entire, elliptic or elliptic-ovate, 6–14.5 cm long and 3.7 cm wide, apically short-acuminate, basally rounded or subacute, dark-green above, lighter beneath, glabrate on both surfaces or slightly pulverulent along the larger veins; petioles 0.8–3.5 cm long, minutely purplish-puberulent. *Inflorescences* axillary, cymose, abundant near the apices of the twigs; cymes solitary, opposite, spreading, 5–9 cm long and 4–8.5 cm wide, loosely flowered; peduncles slender, 2.6–6.5 cm long, densely puberulent; pedicels slender, 7–16 mm long, puberulent; foliaceous bracts none; bractlets and prophylls linear, 2–11 mm long to 1 mm wide or subulate, puberulent. *Flowers* with the calyx pale yellowish-green changing to cream-color and then pure white, fading to yellow or pink, more or less pentagonal during anthesis, 1.8–2 cm long, puberulent, deeply 4-fid, the lobes broadly ovate, 8–10 mm wide, apically acute or short-acuminate; corolla hypocrateriform, dark-red to scarlet or crimson, the tube slender, ca. 2.5 cm long, the lobes wide-spreading or reflexed, 6–10 mm long and 3.5–4 mm wide. *Fruit* drupaceous, glossy-black with a brilliant red aril uniting the 4 pyrenes; fruiting calyx fading to rose-color.

A west tropical African species, native from Senegambia to Congo, now cultivated for ornament throughout the world. It is widely escaped and naturalized in tropical countries of both hemispheres.

In Guyana the leaves and flowers are pounded and then applied to cuts and bruises. "Ala de ángel," "arete de la india," "balao de San Jose," "bandera español," "bleeding heart," "brinco de danea," "clématida," "cornell-flower," "crendolindo," "Danish flag," "fucsia," "jamaiquina," "lágrima de Cristo," "lagrimas de obando," "lazo de amor," "mata vaine," "mil flores," "misteriosa," "pasión de Cristo," "secreto de amor," "southern bleeding-heart," "Thomson glorybower," etc.

PANAMÁ: Panamá, *Bro. Paul 63* (US). CANAL ZONE: Cultivated, *Pittier 2739* (US).

5. **Clerodendrum ligustrinum** (Jacq.) R. Br. *in* Ait., Hort. Kew., ed. 2. 4: 64. 1812.

Volkameria inermis β Ait., Hort. Kew., ed. 1. 2: 364. 1789.
V. ligustrina Jacq., Coll. Bot. Suppl. 118, *pl. 5, fig. 1*. 1796.
Clerodendron culinare Sessé & Moc., Fl. Mex., ed. 2. 151. 1894.
C. fortunatum Sessé & Moc., Fl. Mex., ed. 2. 151. 1894, non *Clerodendrum fortunatum* L., Cent. Plant. 2: 23 [24], as "*fortunata*." 1756.
C. mexicanum Brand., Univ. California Publ. Bot. 3. 391. 1909.

Shrub or low *tree* to 3 m tall, sometimes clambering or vine-like; branches long, slender, obtusely tetragonal or subterete, the young ones brownish, the older ones light-gray, conspicuously lenticellate, the youngest minutely puberulent, later minutely strigillose or glabrous, chartaceous or membranous, elliptic to elliptic lanceolate, 1.5–10 cm long and 0.6–5.1 cm wide, acute or occasionally subacuminate at both ends, entire, glabrous on both surfaces, densely punctate beneath; petioles slender, 5–9 mm long, minutely puberulent, often basally spinescent. *Inflorescences* mostly supra-axillary, rarely terminal, cymose, the cymes solitary, opposite, 3–7.5 cm long and 2–7 cm wide, laxly few-flowered, the terminal ones usually smaller; peduncles widely divaricate, slender, 1.5–4 cm long, minutely puberulent or subglabrate; foliaceous bracts few, caducous, 1–1.5 cm long and 3–7 mm wide, stipitate, minutely puberulent or glabrate, punctate beneath; bractlets and prophylls linear, 1–6 mm long, puberulent; pedicels slender, 3–6 mm long, puberulent, 13 mm long in fruit. *Flowers* with the calyx campanulate, 6–8 mm long, deeply 5-fid, the lobes lanceolate or deltoid, apically acuminate; corolla white, the tube straight, 1–1.2 cm long, the limb spreading, the lobes subequal, shorter than the tube. *Fruit* dry, 1–1.2 cm long and wide when mature, smooth, splitting into 2-seeded halves at maturity.

In marginal forests, thickets, swamps, and the banks of streams and lakes, from northern Mexico to Panama.

In Mexico the leaves are used for flavoring. "Itzimte," "muste."

COLÓN: *Fendler 300* (K). PANAMÁ: *Herb. Miller s.n.* (BM).

5a. **Clerodendrum ligustrinum** var. **nicaraguense** Moldenke, Phytologia 1: 416. 1940.

This variety differs from the typical variety in its leaves and axillary cymes being generally ternate and its leaf-blades being regularly puberulent beneath. The leaf-blades are sometimes irregularly dentate.

Native from Honduras and Nicaragua to Panama, apparently sometimes cultivated.

BOCAS DEL TORO: Old Bank Island, Chiriquí Lagoon, *von Wedel 1955* (MO). Colon Island, *von Wedel 67* (MO). Shepherd Island, Chiriquí Lagoon, *von Wedel 2732* (MO). CANAL ZONE: Canal Zone, *Lindsay 395* (BH, F).

6. **Clerodendrum molle** H.B.K., Nov. Gen. Sp. Pl., ed. folio. 2: 198. 1817.

Shrub, sometimes somewhat climbing to 10 m tall; branchlets slender, gray or buff, subterete, conspicuously lenticellate, densely short-pubescent. *Leaves* opposite or ternate; thin-membranous or chartaceous, drying dark, elliptic, 1–6 cm long and 0.5–3.4 cm wide, apically acute or short-acuminate, basally acute, entire, dark-green above, lighter beneath, finely and sparsely pubescent above, densely short-tomentose or spreading-pubescent beneath; petioles slender, 3–8 mm long, densely pubescent, the lowest 1–2 mm persisting as a corky usually not spinescent protuberance after the leaves have fallen. *Inflorescences* axillary, cymes ternate, solitary in the leaf-axils, divaricate, 3–7 cm long and 1–4 cm wide, loosely 7–9 flowered, pubescent throughout, peduncles slender, 1–3.7 cm long; foliaceous bracts absent; bractlets and prophylls setaceous, ca. 1 mm long; pedicels slender, 1–5 mm long; calyx campanulate, 5-lobed, the lobes ovate, spreading, apically acute. *Flowers* fragrant; corolla hypocrateriform, white or pinkish, the tube usually deep-pink or light-lilac, less than 2.5 cm long, the limb usually white, roseate in the throat, the lobes oblong. *Fruit* corky, baccate or capsule-like, well adapted for floating in the water, sulcate; fruiting-calyx cupuliform, only slightly accrescent.

Native from Panama to Ecuador and the Galapagos Islands, mostly inhabiting the seashore and lower elevations, thickets in low moist ground, rolling scrubland, rocky coastline precipices, lava beds, open woodlands on hillsides, roadsides, the edges of swamps and marshes, and forests.

PANAMÁ: Panamá, *Nee 3* (MA).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 168A. AVICENNIACEAE

HAROLD N. MOLDENKE[2]

Shrubs or trees of maritime regions, mostly inhabiting saline or brackish coastal mangrove lagoons, with pencil-like pneumatophores; branches, branchlets, and twigs commonly terete, prominently nodose, and articulate. *Leaves* decussate-opposite, thick-textured, persistent, petiolate, exstipulate, the blades entire. *Inflorescences* axillary or terminal, determinate and centrifugal (cymose), spicate or subcapitate, the axillary inflorescences mostly paired. *Flowers* sessile, perfect, hypogynous, small; calyx of 5 nearly separate sepals, the sepals ovate and plainly imbricate, unchanged in fruit, subtended by a pseudo-involucre composed of a scale-like bractlet and 2 alternate scale-like prophylla slightly shorter than the calyx and imbricate with each other and with the sepals; corolla regular, campanulate-rotate, 4-parted, the petals connate basally; stamens 4, inserted in the throat of the corolla-tube, equal or subdidynamous; gynoecium 2-carpellate, syncarpous, the ovary compound, but with a free central often more or less 4-winged placenta, the ovules 4, pendant, orthotropous, hanging from the tip of the central columella. *Fruit* a compressed oblique capsule, with a juicy and somewhat fleshy usually tomentellous exocarp, dehiscent by 2 valves, by abortion regularly only 1-seeded; seeds without a testa, the embryo viviparous, the radicle pubescent, the cotyledons 2, folded lengthwise.

Comprises only a single genus, *Avicennia*, with 16 known living species and varieties of the tropics and subtropics of both the Old and New Worlds; one of the chief constituents of almost all coastal mangrove lagoons. Four additional fossil species are known, two from the United States and two from Colombia.

1. AVICENNIA

Avicennia L., Sp. Pl. 110. 1753; Gen. Pl., ed. 5. 49. 1754.

Bontia L. *ex* Loefl., Iter Hisp. 193. 1758.
Upata Rheede *ex* Adans., Fam. Pl. 2: 12 & 201. 1763.
Horau Adans., *op. cit.* 2: 80 & 585. 1763.
Sceura Forsk., Fl. Aegypt.-arab. 37. 1775.
Halodendrum Thou., Gen. Nov. Madagas. 8. 1806.
Halodendron Roem. & Schult., Syst. Veg. 3: 485. 1818.
Hilairanthus Van Tiegh., Jour. Bot. (Morot) 12: 357. 1898.
Bontia P. Br. *ex* Airy Shaw *in* Willis, Dict. Fl. Pl., ed. 7. 146. 1966.

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[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

[2] 303 Parkside Road, Plainfield, New Jersey 07060.

Characters of the family.

a. Inflorescence a lax wide-spreading compound many-branched panicle; pairs of flowers manifestly separated throughout ..... 1. *A. bicolor*
aa. Inflorescence a spike, head, or sparingly-branched simple panicle; flowers mostly closely imbricate, at least at tips of the spikes.
  b. Style very short, shorter than the stamens; leaf-blades mostly elongate-oblong and 3–5 times as long as wide, to 17 cm long and 2.8 cm wide ..... 3. *A. tonduzii*
  bb. Style manifest, exserted from the calyx when the corolla is shed, surpassing the stamens; leaf-blades lanceolate or lanceolate-oblong to elliptic or obovate, usually less than 3 times as long as wide, 4.5–15 cm long and 1.8–4.4 cm wide ..... 2. *A. germinans*

1. **Avicennia bicolor** Standley, Jour. Washington Acad. Sci. 13: 354. 1923.

Shrubs or *trees*, to 13 m high; trunk to 25 cm in diameter; young branchlets glabrous. *Leaves* with the blades broadly elliptic to elliptic-ovate, 7–13 cm long and 3.5–7 cm wide, entire, rounded or obtuse apically, obtuse basally and usually shortly and abruptly decurrent into the petiole, glabrous and lustrous above and with prominent venation, densely covered with a minute whitish tomentum beneath; petioles stout, 4–15 mm long. *Inflorescences* spicate, opposite, the rachis elongate and the pairs of individual flowers 5–8 mm distant from each other, the spikes numerous, forming lax panicles 5–17 cm long, the branches of the panicles minutely tomentellous; bracts and bractlets rounded, obtuse apically, tomentulose. *Flowers* with the corolla ca. 4 mm long, the tube glabrous, the lobes obovate, subtruncate basally, sericeous on the outer surface, glabrous within; style nearly obsolete.

In mangrove lagoons from Chiapas, Mexico, to Panama and the Pearl Islands.

CANAL ZONE: Punta Paitilla, *Bro. Heriberto 206* (NY, US). COCLÉ: Mangrove swamp along outskirts of tidal belt, Aguadulce, *Pittier 4968* (BM, CP, F, K, MOLDENKE, NY, P, US). COLÓN: Porto Pasada, *Williams 78* (NY). DARIÉN: Casaya Island, *Duke 10372* (MO); mangrove swamp near confluence of Río Balsa and Río Tuira, ca. 10 mi. S of El Real on Río Pirre (house no. 22), *Duke 5488* (AAU). PANAMÁ: Panamá, *N. J. Andersson*, 1852 (S); in mangrove swamp, Playa Grande, San José Island, *Johnston 1259* (LL, MO).

According to the label on *Duke 10372*, "Holdridge and I believe there are 2 species in Darién, this is a larger tree with larger leaves and more pronounced white beneath."

2. **Avicennia germinans** (L.) L., Sp. Pl., ed. 3. 891. 1764.—FIG. 1.

Bontia germinans L., Syst. Nat., ed. 10. 2: 1122. 1759.
A. nitida Jacq., Enum. Syst. Pl. Carib. 25. 1760.
A. tomentosa Jacq., *loc. cit.* 25. 1760.
A. elliptica Holm *in* Thunb., Fl. Bras. 3: 37. 1821.
A. floridana Raf., Atlantic Jour. 1: 148. 1832.
A. meyeri Miq., Linnaea 18: 262. 1844.
A. lamarckiana Presl, Bot. Bemerk. 99. 1844.
A. oblongifolia Nutt. *ex* A. W. Chapm., Fl. S. United States, ed. 1. 310. 1860.
A. officinalis α *nitida* (Jacq.) Kuntze, Rev. Gen. Pl. 2: 502. 1891.
A. officinalis β *lanceolata* Kuntze, *loc. cit.* 502. 1891.
Hilairanthus nitidus (Jacq.) Van Tiegh., Jour. Bot. (Morot) 12: 357. 1898.
H. tomentusus (Jacq.) Van Tiegh., *loc. cit.* 357. 1898.

Erect or spreading low *shrubs* or handsome and symmetric slender *trees*, 12–14 (–25) m high, sometimes bushy, usually intermixed with other mangroves but

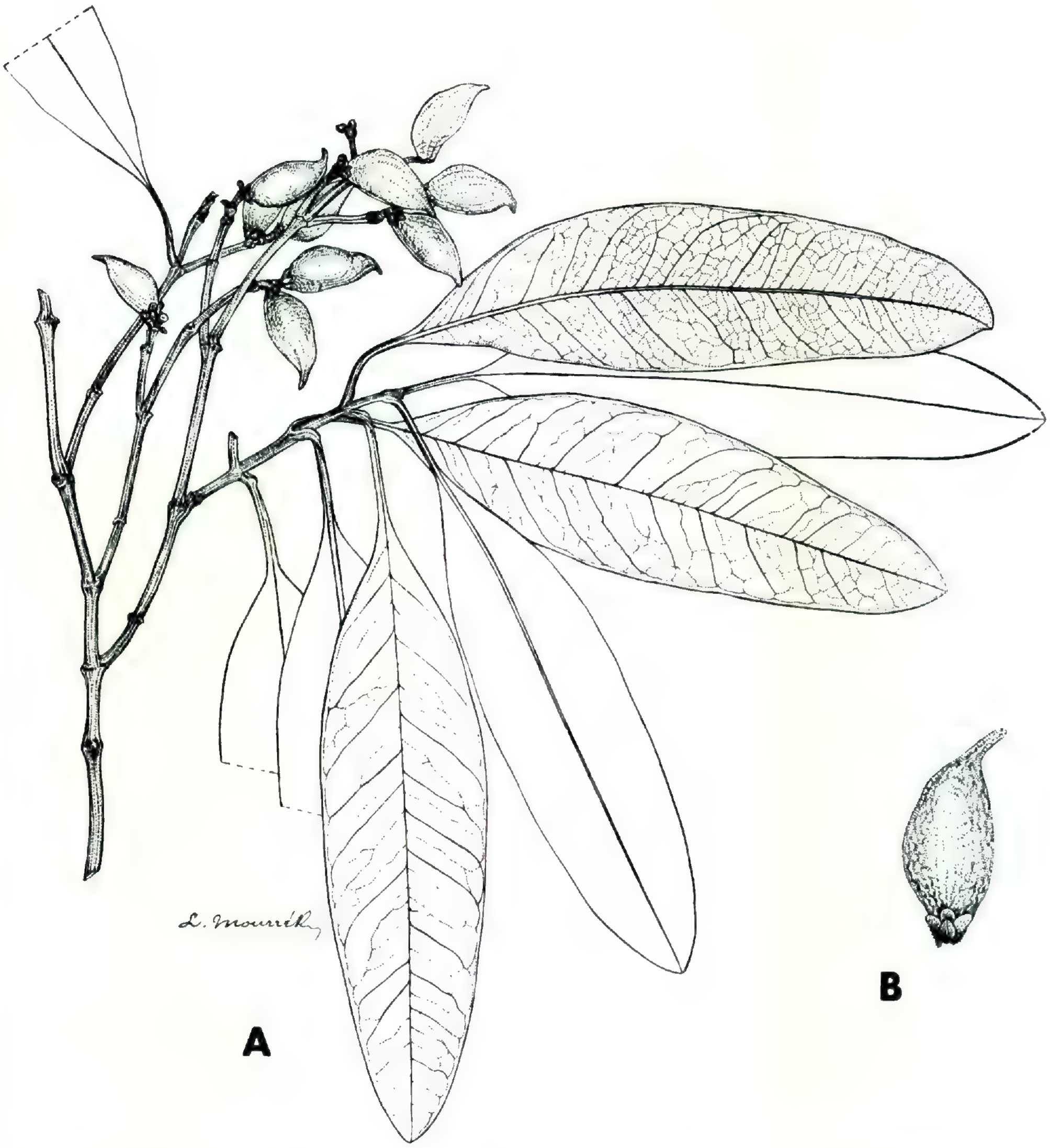

FIGURE 1. *Avicennia germinans* (L.) L.—A. Fruiting branch (× ⅝).—B. Fruit (× 1½). [After *Johnston 1129* (MO).]

normally exceeding them in height; trunk short, to 50 cm in diameter; bole crooked, sometimes to 40 cm diameter at breast height; roots deep-seated; pneumatophores many, small, erect, about as thick as a pencil, projecting 5–10 cm above the water, leafless; stilt-roots absent; bark from black or dark-brown to dark reddish-brown or gray, yellow when scraped, smoothish, sparsely longitudinally cracked or shallowly fissured and rather scaly; branches spreading, crooked; branchlets and twigs slender, often more or less articulate, brownish, more or less tetragonal, often obscurely margined at the angles, glabrous or minutely grayish-tomentellous, often shiny, sparsely lenticellate with scattered corky lenticels; nodes swollen, distinctly annulate. *Leaves* with the blades firmly char-

taceous or subcoriaceous, varying from gray- or bright-green to rich- or dark-green and shiny above, usually pale or gray-silvery beneath, occasionally brunnescent or nigrescent on both surfaces in drying, lanceolate or lanceolate-oblong to oblong, elliptic, or obovate, 4.5–15 cm long and 1.8–4.4 cm wide, entire, acute to blunt or obtuse apically, acute or acuminate to cuneate basally, glabrous but densely impressed-punctulate above, varying from uniformly and densely whitish- or grayish-furfuraceous or tomentellous (with closely appressed furf) to glabrous and more or less punctate beneath, the furf apparently deciduous in patches in some forms; petioles slender, 2–27 mm long, flattened and canaliculate above, convex beneath, mealy or glabrous, often wrinkled in drying. *Inflorescences* axillary and terminal, spicate or subcapitate, the spikes 1.5–6.5 cm long and 1–1.5 cm wide during anthesis, the axillary spikes usually confined to 1 pair at the base of the terminal and shorter than it or another pair in the next lower axil, dense. *Flowers* usually opposite, 1–15 pairs per spike, sessile, sometimes few and distant or close and decussate or densely glomerate-crowded, small, irregular, 1–2 cm wide during anthesis, fragrant, highly nectariferous; bractlets and prophylla light-green, ovate or oblong, sessile, closely appressed to the calyx, obtuse or acute apically, densely sericeous-pubescent; calyx light-green, the lobes ovate, 3–5 mm long and 2–3 mm wide, densely appressed-pubescent outside, glabrous within, in fruit enlarged but not at all incrassate or indurated, 5-parted practically to the base, ca. 9 mm wide, each lobe ovate-lanceolate, ca. 4 mm long and 2 mm wide, acute, densely appressed canescent-strigose outside, glabrous and shiny within; corolla campanulate, yellow or cream to white, apparently yellow when first opening, later turning white, sometimes white with a yellow throat or cream with an orange throat, occasionally creamy on the lobes and brown below, 12–20 mm long and ca. 10 mm wide, parted to about the middle, the tube equaling or shorter than the calyx, practically glabrous, the lobes spreading, unequal, 2–2.5 mm long, oblong or subquadrate, rounded apically, densely cinereous-pubescent outside, velutinous-tomentose within, finally so completely reflexed as to touch the corolla-tube; stamens slightly exserted from the corolla-tube, included by the lobes, finally blackish and conspicuous when the lobes become completely reflexed; style as long as the stamens; stigma bilobed. *Fruit* oblong or elliptic to more or less obpyriform and asymmetric, 1.2–5 cm long and 7–13 mm wide, often turning almost plum-color when exposed to the sun, apiculate apically when young, densely whitish-tomentellous throughout, often also more or less white-strigose, especially apically and on the apiculation.

In mangrove lagoons from Florida and Texas, Bermuda, and the Bahamas, throughout the West Indies, both coasts of Mexico, through Central America, to the coasts of Brazil and Peru; also in the Galápagos and other islands off the coasts of tropical and subtropical America. Highly variable; some of the proposed varieties may prove valid. The extremely long-leaved specimens are closely similar to *A. africana* P. Beauv. and *A. tonduzii* Moldenke. This species needs further and more intensive study.

BOCAS DEL TORO: On sand beach, Changuinola Valley, *Cooper & Slater 81* (US). Water Valley, *von Wedel 987*, in part (MO). CANAL ZONE: Locality unknown, *Allen 1724* (MO, NY); Aspinwall, *Hayes 643* (NY). Salt flats, Balboa, *Standley 30889* (US). Swampy waste

area, Corrosion Laboratory, Miraflores Locks, *Stern et al. 50* (BM, MO). Miraflores Locks area, *Tyson 1261* (MO). COCLÉ: Along outskirts of tidal belt, Aguadulce, *Pittier 4969* (CP, US). COLÓN: Vicinity of Colón, *Cowell 97* (NY). San Blas, *Lay & Collie*, 1825–1828 (BM). Along beach, near sea level, vicinity of Viente Frio, *Pittier 4116* (NY, US). PANAMÁ: Panamá, *Andersson s.n.* (S), *Billberg s.n.* (S), *Duchassaing s.n.* (P), *Hayes*, 1861 (BM), *Seemann s.n.* (BM). San José Island, on shingle beach with *Laguncularia*, end of Canyon Road, *Johnston 1129* (MO). Rocky beach, Naval Cove, *Erlanson 120* (NY).

This species is commonly known as "white mangrove" (fide *Cooper & Slater 81*).

3. **Avicennia tonduzii** Moldenke, Phytologia 1: 273. 1938.

Trees, to 11.5 m high; branchlets and twigs slender, obtusely tetragonal or subterete, articulate, the youngest parts densely matted-tomentellous with flavidulous puberulence, the older parts less densely so to glabrate, the youngest parts wrinkled in drying, the nodes swollen and annulate; leaf-scars conspicuous. *Leaves* numerous, the blades bright-green and somewhat shiny above, gray beneath, oblong or elongate-oblong to elliptic, 7.3–17 cm long and 1.6–4.8 cm wide, entire, obtuse or blunt to acute apically, acute to acuminate or long-attenuate basally and prolonged into the petiole, densely and minutely puberulent and impressed-punctate above, becoming glabrescent in age, uniformly densely matted-tomentellous beneath; petioles 8–20 mm long, densely matted-tomentellous or appressed-puberulent, not noticeably ampliate basally, mostly wrinkled-striate in drying. *Inflorescences* axillary and terminal, paniculate, 3–6 cm long and wide, usually regularly several-branched from the base, the branches many-flowered, the axillary ones crowded in the uppermost axils, 2–3 cm long and 1–2 cm wide, the terminals 3–5 cm long and 3.5–4 cm wide; peduncles, rachis, and inflorescence-branches densely matted-tomentellous and wrinkled-striate like the petioles; bractlets ovate, a pair subtending each pair of inflorescence-branches. *Flowers* sessile; prophylls 3, ovate, ca. 2 mm long and 1.5 mm wide, strigose at the center, villous-tomentose toward the margins, rounded or obtuse apically, simulating and closely appressed to the sepals, imbricate; sepals 5, free, imbricate, broadly elliptic or subrotund, ca. 2.5 mm long and wide, rounded apically and basally, densely villous-tomentose; corolla hypocrateriform, the tube broadly cylindric, straight, ca. 1 mm long, glabrous, the limb 4-parted, the lobes equal, wide-spreading during anthesis, narrowly elliptic-lingulate, ca. 3 mm long and 1.5 mm wide, rounded apically, densely tomentose; stamens inserted ca. 0.5 mm above the base of the corolla-tube, equal, exserted, the filaments ca. 1.5 mm long, glabrous; ovary ovate-subglobose, ca. 1.25 mm long and wide, densely appressed-villous, the style 0.75 mm long, much shorter than the stamens.

In mangrove swamps, Costa Rica to Colombia. This species greatly resembles the west African *A. africana* P. Beauv.

PANAMÁ: Taboga Island, *Pittier 3614* (NY, US).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 180. CAPRIFOLIACEAE[1]

W. G. D'ARCY[2]

Herbs, *shrubs*, *trees*, or *vines*, unarmed, mostly pubescent with short simple hairs and sometimes also with multangulate stellate hairs, mostly with short stalked glands which often dry reddish-brown, the plants sometimes sarmentose or with a perennial rhizome, the pith mostly large, hollow or solid, often soft. *Leaves* deciduous or evergreen, mostly opposite, sometimes ternate, and some of the leaves sometimes connate-perfoliate, entire or imparipinnately compound, sometimes lobed, the leaves and leaflets mostly serrate or dentate, the teeth glandular-callose at the tips, pubescent or glaucous beneath, sometimes gland-bearing; stipules present or absent, often small or caducous or represented by an interpetiolar ridge; petiolules sometimes stipellate; bud scales present or absent. *Inflorescences* terminal or axillary, rarely solitary, mostly several- or many-flowered in panicles, cymes, or sessile verticels, in a number of genera the individual flowers ultimately arranged in pairs and sometimes the paired ovaries connate; bracts and braceoles usually present and sometimes connate in pairs, often glandular, sometimes accrescent in fruit. *Flowers* fragrant, bisexual or in a few species with larger neuter flowers at the periphery of the inflorescence, (3–)4–5(–6)-merous, regular or irregular; calyx-tube globose, campanulate, or tubular, adnate to the ovary and enveloping it in fruit, glabrous or pubescent, sometimes glandular or glaucous, the lobes mostly small and spreading but in a few genera accrescent and subfoliaceous in fruit; corolla epigynous or perigynous, mostly 4–5 lobed, regular to strongly irregular and 2-lipped, 4 lobes forming the upper lip, ranging from rotate-campanulate to tubular and salverform, the lobes rounded apically, quincuncial or rarely valvate in bud, the tube sometimes gibbous, saccate or ventricose, often with 1–5 elongate nectaries within; stamens as many as the corolla lobes or in some genera reduced to 4 or 2, inserted equally or unequally but rarely didynamous on the corolla tube and alternate with the corolla lobes, the filaments glabrous or pubescent, unappendaged but variously thickened, straight or folded in bud, the anthers free, mostly dorsifixed and versatile, exserted or included, ellipsoid to linear, the thecae parallel, 2–4-loculed, dehiscing longitudinally or introrsely, sometimes extrorsely, the connective not thickened or protruding; ovary half or more inferior, sometimes connate with that of the adjacent flower, the locules 1–8, often asymmetrical with respect to the floral axis, the ovules 1–several

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[1] Assisted by National Science Foundation Grant GB-362-02X.

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ANN. MISSOURI BOT. GARD. 60: 155–167. 1973.

per ovule, those in some locules regularly aborting, pendulous from the apex of the locule or rarely axile, anatropous, the style (including superior portion of the ovary) stout-conical to elongate and linear, the stigmas as many as the locules and more or less connate, unequal or equal, sometimes capitate and faintly lobed; a perigynous disc inconspicuous or absent. *Fruit* mostly a 1–several-seeded fleshy or juicy berry or drupe, rarely a longitudinally dehiscent capsule; seeds with a bony or coriaceous testa, rarely minute, the endosperm copious, fleshy, sometimes ruminate, rarely granular, the minute embryo straight, situated at one end of the seed.

A family of about a dozen genera with about 400 species, most in the two genera *Lonicera* and *Viburnum*. Most species in the family are in the north temperate zone and on tropical mountains, while the greatest number of genera have species in the regions flanking the mountains of Asia. Two genera are native to Panama, and another is known by one introduced species. The type genus is *Lonicera* L. (*Caprifolium* Tourn.).

Plants in the Caprifoliaceae are usually distinguishable by their opposite leaves, poorly developed stipules, perygynous 4–5-parted perianth, few or solitary pendulous ovules, and more or less united styles. The family may not be wholly natural, and a number of botanists have separated various genera into distinct families. Sometimes considered to have a close affinity with the Rubiaceae, at least some genera are very similar to the Araliaceae.

Several species are grown in Panama as ornamentals, and one is used for medicinal purposes. Some species have edible berries.

Various parts of many species are used in various regions of the world for medicinal purposes and some yield dyes. A number of species have edible fruits. From the viewpoint of toxicity, however, the Caprifoliaceae has a mixed reputation, and cases of slight to lethal poisoning of stock and man have been attributed to plants of this family. In Panama, *Sambucus canadensis* var. *laciniata* is used ornamentally and medicinally.

a. Vines; flowers in many-flowered compound cymes; corollas distinctly 2-lipped, tubular-salverform, more than 2 cm long ..... 1. *Lonicera*
aa. Shrubs or trees; flowers in 2-flowered dichasia; corollas regular, rotate-campanulate, less than 1 cm long.
  b. Leaves imparipinnate; fruits mostly 4–5-seeded ..... 2. *Sambucus*
  bb. Leaves simple; fruits 1-seeded ..... 3. *Viburnum*

1. LONICERA

Lonicera L., Sp. Pl. 173. 1753. TYPE: *L. caprifolium* L.[3]

Vines, shrubs, or small trees, mostly pubescent with simple, several-celled hairs, some with transparent terminal glands which often dry reddish-brown; branches fistulose or solid. *Leaves* evergreen or deciduous, simple, mostly entire, paired, some pairs sometimes connate-perfoliate, glabrate or pubescent, sometimes glaucous beneath, membranaceous, coriaceous, or succulent, petiolate, mostly estipulate, bud scales often present. *Inflorescences* mostly numerous, pedunculate,

[3] A list of generic synonyms is provided by Hutchinson, *Genera of Flowering Plants* 2: 87. 1967. None of these names has been used for Panamanian material.

2-flowered cymes (dichasia) and bracteate and bracteolate or in sessile verticels of 3-flowered dichasia, the bracts sometimes foliaceous, the bracteoles sometimes connate and enveloping the ovary; pedicels short of wanting. *Flowers* fragrant, often showy, bisexual, 5-merous; calyx-tube elliptical or rotund, glabrous or pubescent, sometimes glaucous, the lobes small or obsolete; corolla variously colored, sometimes fading to a different color, rarely regular, mostly strongly 2-lipped and slightly ventricose or variously saccate, gibbous, or spurred, glabrous or pubescent and with 1–5 nectaries along the inside of the tube, the lobes quincunical in bud; stamens 5, subequal, the filaments slender, the posterior 3 inserted in the corolla tube slightly above the anterior 2, the anthers oval to oblong or narrowly elliptical, straight in bud but in flower sometimes recurving at both ends, dorsifixed and versatile, mostly exserted, the 4 locules sometimes partly confluent, dehiscing introrsely by longitudinal lateral slits; the ovary inferior, sometimes connate with that of the adjacent flower, 2–3(–5)-loculed, the ovules 3–8 per locule, pendulous from the top of the ovary, anatropous, the style elongate, slender, glabrous or pubescent, the stigma small, indistinctly-lobed. *Fruit* a juicy or fleshy few-seeded berry, often shiny and bright-colored, rarely enveloped by accrescent bracteoles, mostly surmounted by the persistent calyx lobes; the seeds compressed, ovoid with smooth or granular testa, the endosperm fleshy, the embryo terete, minute, straight or slightly curved, the cotyledons terete.

A genus of nearly 200 species, mostly located in north temperate regions. The most unspecialised species, which grow in central Asia, are alpine shrubs with nearly regular, 5-parted corollas, and short styles, and are hardly distinguishable from the mainly North American genus *Symphoricarpos*. From such unspecialised groups, *Lonicera* ranges to festooning vines with strongly 2-lipped corollas and long-exserted styles, as in the single species which is naturalised in Panama.

Many species are cultivated in temperate regions for the fragrance of their showy flowers and their attractive foliage. The fruits also are important foods for wildlife. The Panamanian species is of mixed benefit; an attractive ornamental, it is also a persistent weed of mountain gardens and pastures.

Useful reference:

Rehder, A. 1903. Synopsis of the genus *Lonicera*. Annual Rep. Missouri Bot. Gard. 14: 27–232.

1. **Lonicera japonica** Thunb., Fl. Jap. 89. 1784. TYPE: (Not seen).[4]—FIG. 1.

Twining *vine* or shrub to 10 m long or more, trailing at ground level or festooning on shrubs or small trees; stems terete, sometimes reddish on one side, loosely to densely pubescent with slender and stout simple hairs to 1 mm long, some hairs gland-tipped, the glands mostly transparent but drying reddish-brown, the hairs on the young parts retrorse. *Leaves* opposite, not connate, entire (lobed on juvenile plants), ovate, oblong, or elliptical, mostly widest at the middle or below, apically acuminate, acute or obtuse, often mucronulate, basally rounded, truncate

[4] For a list of synonyms see: Rehder, A. 1903. Synopsis of the genus *Lonicera*. Annual Rep. Missouri Bot. Gard. 14: 27–232. None of these names has been used for Panamanian material.

FIGURE 1. *Lonicera japonica* Thunb., habit with flowers (× ⅗). [After *D'Arcy* 5335 (MO).]

or obtuse, often slightly oblique, mostly 4–7 cm long, ca. half as wide, glabrate to pilose with stout, simple, mostly eglandular hairs, the hairs with expanded bases above, the margin ciliate, the veins ca. 4 on each side of the midvein, the minor venation reticulate, conspicuous beneath, often obscure above; petiole 3–10 mm long, pilose, lenticular in cross section; small but well developed shoot buds evident in the leaf axils. *Inflorescences* numerous, axillary, appearing near the ends of the branches, pedunculate solitary pairs (dichasia) of closely positioned flowers subtended by pairs of foliaceous bracts; peduncles 1–2 cm long, not much altering in fruit, slightly compressed dorsally, pilose with short and long simple hairs, many hairs glandular; bracts variable in size, mostly 2–3 cm long and resembling the leaves; bractlets obtuse, about half to as long as the ovaries (ca. 1 mm), conspicuously ciliate with stout, 1 mm long hairs, sometimes hairy dorsally; pedicels wanting. *Flowers* white fading yellowish, fragrant; calyx tube enclosing the ovary, the lobes ca. 1 mm long, lanceolate-deltoid, prominently ciliate, glabrous dorsally and ventrally; corolla 4–5 cm long, strongly 2-lipped, the tube ca. 2 cm long, slender, straight and broadening slightly upward, not saccate or ventricose, pubescent outside and in, with a yellow, gland-dotted, nectary extending along the inside of the tube from the base to about halfway up and situated along the junction of one of the sutures of the lower lip, the limb equalling or slightly exceeding the tube, the upper lip 4-lobed about halfway down, the lower lip distinct from the base of the limb; stamens sub-equal, the filaments white, glabrous, straight, tapering slightly near the apex, the upper 3 inserted at a slightly higher level than the dorsal 2, the anthers dorsifixed at ca. the middle, ca. 4 mm long, elongate, straight in bud but soon recurving at the ends into a 'U' shape; ovary 1.5–2 mm long, 3-loculed, the ovules 2–3 per locule, the style glabrous, the stigma green, discoid, not evidently lobed. *Fruit*[5] a black, juicy, shiney berry crowned by the persistent calyx.

Lonicera japonica is an almost cosmopolitan weed, transported to many countries by man as a cultivated ornamental. It belongs to a group of species (subsect. *Longiflorae* Rehd.) native to the Old World and itself native to eastern Asia. "Japanese honeysuckle" (English), "madreselva" (Spanish).

CHIRIQUÍ: Cerro Punta, ca. 7000 ft, *Blaisdell 378* (MO). Along trail N of Cerro Punta, abundant locally, *Croat 10502* (MO). Weed in vegetable patch above Nueva Suisa, 6000 ft, *D'Arcy 5335* (C, MO, UCWI).

2. SAMBUCUS

Sambucus L., Sp. Pl. 269. 1753. TYPE: *S. nigra* L.

Herbs, *shrubs*, or *trees*, sometimes sarmentose; branches with a soft, solid pith, the twigs glabrous or pubescent, often drying striate, sometimes purplish. *Leaves* opposite, evergreen, not connate, imparipinnately-divided, the leaflets finely toothed, glabrous or pubescent with simple hairs and sometimes with subsessile glands which may dry reddish; the petiole sometimes gland-bearing, estipulate or with stipule-like glandular appendages, often slightly clasping the stem; petiolules short, sometimes stipellate. *Inflorescences* terminal or axillary, held above

[5] No fruiting material was seen from Panama. Details of the fruit are taken from *Eggert*, 16 Sept. 1896 (MO), from Panola County, Mississippi.

the leaves, panicles or compound umbellate cymes or variations between these types, bracts and bracteoles sometimes present, some flowers without pedicels. *Flowers* bisexual, numerous, small, fragrant, mostly white or reddish; calyx campanulate, the tube adnate to the ovary and enclosing it in fruit, the lobes small, mostly glabrous, persistent on the fruit; corolla perigynous, campanulate-rotate, deeply-lobed, the lobes rotund, quincuncial or rarely valvate in bud, glabrous or with a few hairs near the apex of the tube; stamens equal, the filaments inserted on the short corolla tube, glabrous, the anthers ellipsoidal, basi-fixed, opening extrorsely by longitudinal lateral slits; ovary immersed more than half-way in the calyx tube, 1–5-locular, the ovules 1 per locule, pendulous from the apex of the locule, anatropous, the superior portion (style) glabrous, stout and conical, the stigmas as many as the locules, often unequal, more or less connate; disc wanting. *Fruit* a 1–5-seeded juicy berry; the seeds lenticular, slightly trigonous, rugose, the dorsal surface widest.

About 20 species in the temperate zones and a few on tropical mountains. Most species are found in the north temperate zone, and some range into the Arctic. Major taxonomic distinctions are in the structure of the inflorescence, color of the pith, and appearance of the fresh fruits. Several sections are recognised in the genus, and the two Panamian species belong to sect. *Sambucus*, which includes both New and Old World species.

Features of wood histology, inflorescence structure, and general appearance have suggested to several writers that this genus may not belong in the Caprifoliaceae. In many respects, *Sambucus* is similar to the Araliaceae.

In other parts of the world, the flowers and leaves are used medicinally, and the berries are sometimes used for making wine. The roots and some other parts of the plants are reputedly poisonous and uncooked berries may cause nausea.

Useful references:

Schwerin, F. 1909. Monographie der Gattung *Sambucus*. Mitt Deutsch. Dendrol. Ges. 18: 1–56.

———. 1909. Revisio generis *Sambucus*. op. cit. 29: 194–231.

a. Leaves membranaceous, mostly 3–5-foliolate, the veins mostly 4–5 on each side of the midvein, the serrations irregular and not extending into the obtuse basal ⅕ of the leaf; shrub not exceeding 5 m tall; not known to fruit in Panama ... 1. *S. canadensis* var. *laciniata*

aa. Leaves fleshy, mostly 7–11-foliolate, the veins mostly 7–10 on each side of the midvein, the serrations evenly fine and extending into the rounded leaf base; shrub or tree to 20 m tall; berries globose, 7–9 mm in diameter, abundantly produced in Panama ... 2. *S. peruviana*

1. **Sambucus canadensis** var. **laciniata** A. Gray, Syn. Fl. N. Amer. 1(2): 9. 1844. TYPE: Indian River, Florida, *Palmer*, 1874 (MO).

S. simpsonii Rehd. *in* Sarg., Trees & Shrubs 2: 187, *t. 175*. 1911. TYPE: Bradentown, Manatee Co., Florida, *Simpson*, "June 1910" (A).

S. intermedia var. *insularis* Schwerin, Mitt. Deutsch. Dendrol. Ges. 18: 38. 1909. TYPE: Not seen.

Shrub or *herb-like tree*, to 4 m tall, sarmentose; stems terete, glabrous, usually drying with a striate or furrowed appearance; twigs green or purplish, glabrous

or soon glabrescent, the pith white. *Leaves* 3–5(–10)-foliolate; leaflets mostly ovate, obovate, or elliptical, apically acuminate, basally obtuse, 4–11 cm long, the margins irregularly serrate except the basal ⅕, glabrate or sparingly pubescent on the veins, sometimes with occasional subsessile glands; the veins mostly 4–5 on each side of the midvein; petiolules short, to 8 mm long, mostly pubescent above and glabrate on the sides and beneath; the petiole green or purplish, glabrate, somewhat clasping at the base, often with pairs of glands along its length and at the base where they resemble stipules. *Inflorescences* showy, 2–4 times compound glabrate cymes situated above the leaves on elongate peduncles to 16 mm long, the first division an umbel of 5 unequal branches often subtended by small glandular bracts; pedicels to 5 mm long or absent, glandular bracteoles sometimes present. *Flowers* white, fragrant; calyx ca. 1 mm long, the tube campanulate, glabrate with a few minute hairs, lobed to ca. ⅓ of the way down, the lobes obtuse, glabrous, persistent on the fruit; corolla campanulate-rotate, ca. 2 mm long (3–4 mm in diameter), sometimes with a few hairs near the apex of the short tube, deeply-lobed, the lobes rotund, glabrous, quincuncial in bud; stamens exserted, equal, the filaments glabrous, the anthers ca. 0.75 mm long, ellipsoidal, often dehiscing before the corolla opens; the ovary (1–)4–5-loculed, the style (superior portion of the ovary) glabrous, the stigmas as many as the locules, more or less connate, often unequal. *Fruit* unknown in Panama.

Sambucus canadensis ranges from Canada to Panama and has been introduced to South America. The var. *laciniata* which occurs in Panama is native to southern Florida, the Greater Antilles, and parts of Central America, but it has been widely planted throughout this range as an ornamental and medicinal plant so that the boundaries of its natural range are indeterminate. This variety is not known to fruit in Panama nor in the Antilles, but as it roots readily from trash and may be long persistent after planting by man, plants are often found well away from currently inhabited sites. It is distinct from var. *canadensis* in its sturdier trunks, reduced pubescence, and usually smaller and more irregularly serrate leaves. There is also a strong tendency for one or more of the basal leaflets to be lobed or divided, resulting in a partial double pinnation. Much Panamanian material of this variety has been misdetermined as *Sambucus mexicana* var. *bipinnata* (Cham. & Schlecht.) Schwerin. Both *S. mexicana* Presl and the variety *bipinnata* are distinct in having densely pubescent petiolules and petioles and usually greater overall pubescence. This pubescence includes hairs of different lengths, some glandular and some eglandular.

Although a lectotype has not been chosen for *Sambucus intermedia* var. *insularis* Schwerin, the selection must be from one of the several Antillean collections listed in the protologue and not one of the Central American collections which include the lectotype of *S. oreopola* Donn. Sm., a different variety.

In the Chiriquí mountains *Sambucus canadensis* var. *laciniata* is much planted as an ornamental and for the reputed medicinal properties of the roots. Escapes are frequent. "Elderberry" (English), "sauco" (Spanish).

CHIRIQUÍ: Near El Boquete, 900 m, *Allen 1014* (MO). Detrás de cabaña de Florida State University ca. 6 km del pueblo de Cerro Punta, *Correa 1237* (MO, PMA). Near Audubon Cabin (Volcán District), *Croat 13789* (F, MO). Chiquero, Boquete District, 4500 ft, *Davidson*

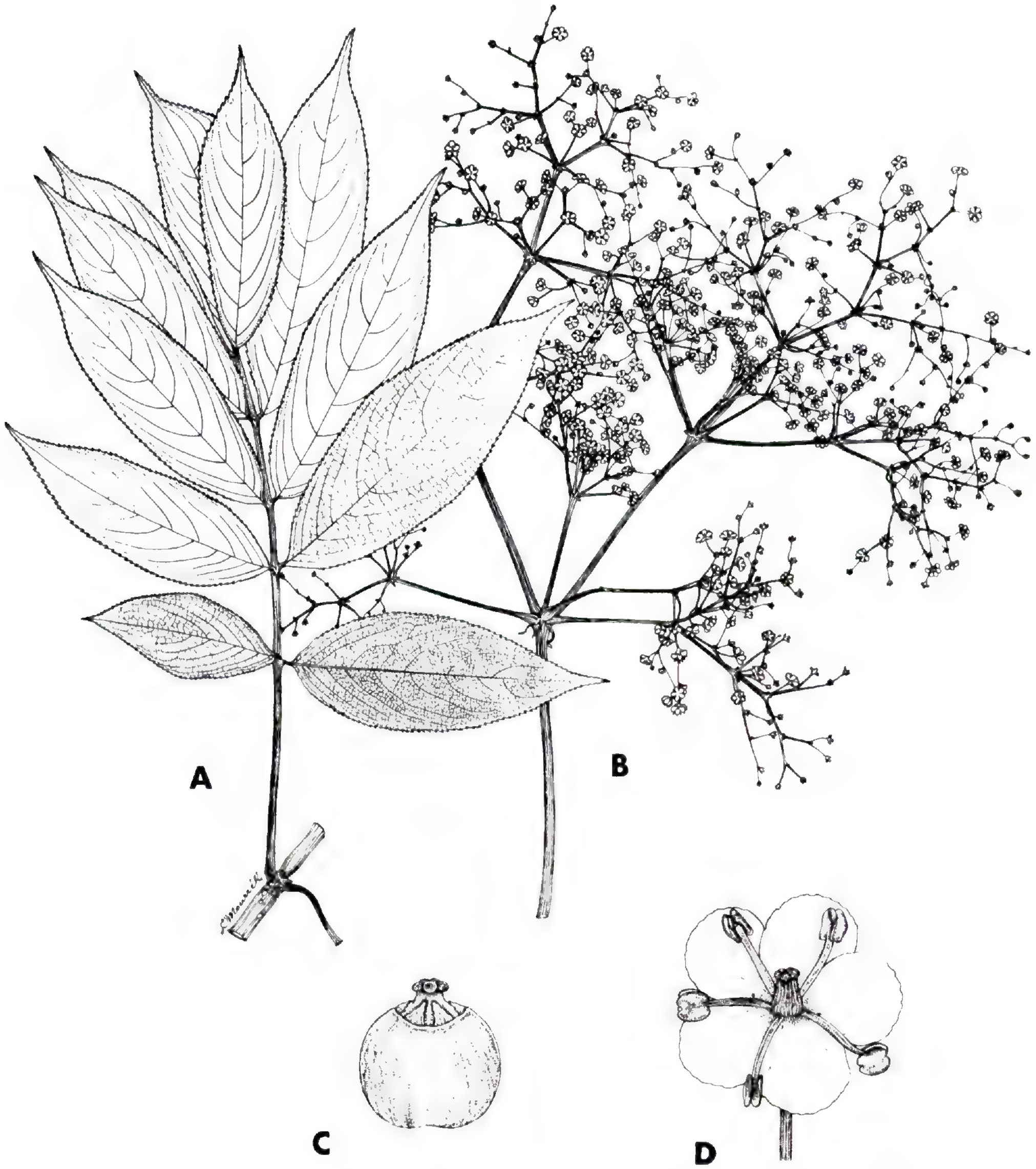

FIGURE 2. *Sambucus peruvianum* H.B.K.—A. Leaf (× ⅜).—B. Inflorescence (× ½).—C. Berry (× 5).—D. Flower (× 6). [After *D'Arcy 5347* (MO.)]

542 (A, MO). Boquete along roadside, 4300 ft, *Hayden 157* (MO). Frequent in moist sunny areas 1 mi. E of Cuesta de Piedra 2880 ft, *Tyson 910* (MO).

2. **Sambucus peruviana** H.B.K., Nov. Gen. Sp. 429. 1818. TYPE: Peru, *Bonpland* (not seen).—FIG. 2.

Shrub or *tree*, to 20 m tall, stems terete, glabrous, usually drying finely striate; the pith white or slightly buff-colored. *Leaves* somewhat fleshy, mostly 7–11-foliolate; leaflets ovate, oblong or lanceolate, apically acuminate, mostly rounded basally, sometimes obtuse, 8–20 cm long, the margins evenly fine-serrate almost to the base, above glabrous except for minute simple hairs on the midvein, beneath

finely pubescent with short erect often curved hairs, especially on the veins, the veins mostly 7–10 on each side of the midvein; petiolules short, to 15 mm long, glabrate sometimes with stipule-like processes at the base, petiole glabrous, somewhat clasping at the base. *Inflorescences* large and showy, 3–5-times compound, glabrate cymes to 40 cm in diameter, situated above the leaves on elongate peduncles, the first division an umbel of 5 unequal branches often subtended by inconspicuous glandular bracts; pedicels to 8 mm long or absent, minute bracteoles mostly present, the nodes of the inflorescence minutely pubescent with glandular or eglandular hairs, the glands mostly drying dark reddish. *Flowers* white, calyx ca. 1 mm long, the tube companulate, glabrous, often glandular, lobed to ca. ⅓ of the way down, the lobes glabrous, obtuse, persistent in fruit; corolla campanulate-rotate, ca. 2 mm long (3–5 mm in diameter), deeply-lobed, the lobes rotund, quincuncial in bud; stamens exserted, equal; ovary 5-loculed, the style (superior portion of the ovary) glabrous, sometimes expanding to 1 mm long in fruit, the stigmas 5, connate in a ring, nearly equal. *Fruit* a juicy globose berry 7–9 mm in diameter, smooth, shiny, without trace of a bloom or furrows when fresh, when dry turbinoid, 2 mm in diameter and 3–4 mm high, recessed beneath with 4–5 prominent longitudinal ridges; seeds 5.

Sambucus peruviana ranges from Argentina to at least as far north as Costa Rica. In Panama it is known only at upper elevations in the Chiriquí mountains, where it occurs in pastures and in the forests. This species is the largest in the genus, reaching the proportions of a substantial tree. The leaves, inflorescences, and fruits are also larger than in any other species in the genus. Quite distinctive in the field, *S. peruviana* may be difficult to distinguish on the herbarium sheet from some forms of *S. canadensis*. The fine, even serration of the leaves which continues into the rounded leaf base will distinguish *S. peruvianum* from *S. canadensis* var. *laciniata*, but these features are also present in Costa Rican specimens which have been identified as *S. canadensis* var. *oreopola* (Donn. Sm.) Rehd. Fruits of South American *S. peruviana* reportedly ripen black, but collectors' notes on Panamanian specimens mentioned red fruits. The only fresh fruits seen (*D'Arcy 6572*) were immature and pinkish-yellow.

CHIRIQUÍ: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 5011* (MO). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2630* (MO, SCZ). Pastures along road S of Cerro Punta, *Croat 10432* (F, MO). In low wet area by dwellings, Nueva California, *D'Arcy 5347* (C, MO, PMA). In overgrown pasture area between Cerro Punta (town) and Cerro Respinga, 6400 ft, *D'Arcy & D'Arcy 6572* (AC, MO, UCWI). Boquete, Cerro Horqueta, dense woodland in cloud forest, 5000–6000 ft, *Dwyer & Hayden 7699* (MO). Cerro Horqueta, cloud forest, 6000 ft, *Hagen & Hagen 2097* (MO). Streamside near Nueva Suisa ca. 2 mi. E of Cerro Punta, 5700 ft, *Wilbur et al. 13010* (PMA).

3. VIBURNUM

Viburnum L. Sp. Pl. 267. 1753. TYPE: *V. lantana* L.

Oreinotinus Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1860: 211. 1861.[6]

Shrubs or *trees*, sometimes scandent; branches solid or with soft pith, the twigs terete, often pubescent. *Leaves* deciduous or evergreen, in some species with bud

[6] A list of generic synonyms is provided by Hutchison, *Genera of Flowering Plants* 2: 85. 1967. Only the above names have been used for Panamian material.

scales, opposite or ternate, simple, not connate, the margins entire or dentate, the teeth often callose-glandular, mostly pubescent with simple, stellate, or lepidote hairs and often with reddish-drying glands, often penninerved; petiolate, the petioles often glandular, appendaged, and clasping; stipules mostly inconspicuous or wanting. *Inflorescences* axillary or terminal, compound cymes or rarely panicles, bracts and bracteoles mostly present, sometimes sub-foliaceous, the pedicels or peduncles often articulating at the base. *Flowers* white or rose, fragrant, bisexual and regular or the outer flowers of the inflorescence sometimes neuter and irregular; calyx tube ellipsoidal or cylindrical, pubescent, glandular or glabrous, adnate to the ovary, the lobes mostly persistent, equalling the tube or shorter; corolla perigynous, mostly campanulate, sometimes rotate or tubular deeply 4–5-lobed, the lobes quincuncial (? or imbricate) in bud; stamens equal, the filaments inserted at the base of the corolla tube, straight and sometimes compressed or variously thickened along their length, the anthers exserted, dorsifixed and versatile, ellipsoidal, opening introrsely; ovary immersed halfway or more in the perianth tube, 3–1-locular, the locules not radially symmetrical with respect to the floral axis, the ovules 1 per locule, pedulous from the apex of the locule, anatropous, the superior portion (style) glabrous, glandular, or pubescent, persistent on the fruit, the stigmas 3, free or more or less connate, rarely appendaged; disc absent. *Fruit* a baccate drupe, sometimes brightly colored, globose, ellipsoidal, ovoid, or sometimes compressed, 1-seeded (by abortion); the seeds oblong, compressed, grooved, or the margins inflexed, the raphe lateral, the endosperm fleshy and rarely ruminate, the embryo minute, straight, situated at the apex of the seed, the cotyledons semi-terete.

A genus of about 100–200 species of wide distribution, numerous in the north temperate zone and on tropical mountains, rare in the Antilles, absent from New Zealand and Australia, and rare in eastern and southern South America. The Panamanian species are closely related and are restricted to the uplands of the Chiriquí Mountains. The fruits of some species are edible.

Useful reference:

Morton, C. V. 1933. The Mexican and Central American species of *Viburnum*. Contr. U. S. Natl. Herb. 26: 339–366.

a. Leaves glabrate, if pubescent then not felty-tomentose, the margins entire or with only a few teeth; pedicels and peduncles slender, pubescent or glabrate but not tomentose; drying dark ..... 1. *V. costaricanum*
aa. Leaves felty-tomentose with numerous glandular-cellose teeth; pedicels and peduncles stout, tomentose ..... 2. *V. stellato-tomentosum*

1. **Viburnum costaricanum** (Oerst.) Hemsl., Biol. Cent. Amer. Bot. 2: 2. 1881. —FIG. 3C.

Oreinotinus costaricanus Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1860: 290. 1861. TYPE: Irazú, Costa Rica, *Oersted 7808* (C, not seen).
Virburnum conspectum Morton, Contr. U. S. Natl. Herb. 26: 349. 1933. TYPE: Panama, *Pittier 3268* (GH).

Shrub or *tree* to 15 m tall; branches terete, the bark various but sometimes grey and finely striate, sometimes with yellowish, corky excrescences, mostly

glabrous, the twigs 4–15 mm long, sparsely to densely and mostly appressed-pubescent with simple hairs and sessile, pauciradiate stellate hairs, drying ochraceous or dark, yellowish, or greyish-brown; bud scales glabrous to tomentose, the outer pair ca. 1 mm long, the inner pair ca. 3 mm long. *Leaves* 5–9 cm long, entire or apically toothed, ovate, often with 1 or 2 pairs of glands near the base, apically acuminate, basally acute, acuminate, obtuse, or rounded, glabrate with sessile pauciradiate hairs on the principal veins above and beneath, mostly barbellate in the vein axils beneath, sometimes shiny, sometimes conspicuously reticulate-veined beneath; petioles 4–16 mm long, puberulent to strigose, channelled above; stipules absent. *Inflorescences* 2–4-times compound cymes 4–8 cm in diameter, terminal, the bracts deciduous, oblong, ciliate or sometimes strigose overall, 1–3 mm long, the bracteoles entire, obtuse, very short or sometimes exceeding the calyx tube, ciliate; peduncle and pedicels drying brown, pubescent with more or less appressed, sessile stellae and with simple hairs. Flowers white, strongly fragrant; calyx ca. 1 mm long, the tube cylindrical or obconical, mostly glabrate, lobed to ca. ¼ of the day down, the lobes obtuse or rounded, ciliate but otherwise glabrate; corolla campanulate, glabrate with a few hairs near the apex of the tube, ca. 2.5 mm long, lobed to ⅔ of the way down, the lobes quincuncial in bud and rounded; stamens exserted, the filaments narrowed apically, glabrous, the anthers ca. 1 mm long; superior portion of the ovary (style) glabrous or sometimes with occasional minute simple hairs, conical with indistinct longitudinal ridges, the stigmas 3, more or less connate, unappendaged. *Fruit* unknown.

This species is restricted to the uplands of Costa Rica and neighboring mountains in Panama. All collections seen are from above 1100 m elevation.

Pittier 3268 (GH) differs from most other collections in its broader leaves, barbellate vein axils and few rayed-stellate hairs, but several other collections intergrade in these characters. Therefore, *Viburnum conspectum* Morton is considered conspecific with *V. costaricanum*, although it may warrant recognition at some infraspecific level.

CHIRIQUÍ: North forested face of Cerro Copete, an eastern spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4859* (MO). Edge of Forest, La Popa above Boquete, 5500 ft, *D'Arcy & D'Arcy 6450* (C, MO, NA, PMA, UCWI). Scattered trees in mature forest and fedded areas, Cerro Respinga above town of Cerro Punta, 8400 ft, *D'Arcy & D'Arcy 6559* (ADW, BIRM, C, CAL, COI, COL, CORD, DAO, DUKE, F, FSU, G, GH, K, L, LE, M, MO, MPU, NY, P, PMA, POM, PRE, R, TH, UCWI, US, VEN, WIS). Volcan de Chiriquí, Boquete District, 7000 ft, *Davidson 921* (MO). Boquete District, 8500 ft, *Davidson 968* (MO). Finca Collins near Boquete, *Blum & Dwyer 2562* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 333* (MO, US). Boquete District, 7000 ft, *Davidson 921* (A, MO, US). Volcán de Chiriquí, Boquete District, 8500 ft, *Davidson* (flowering July) *968* (US). Boquete, 5500 ft, *Dwyer 6966, 7007* (both MO). Cerro Horqueta NW of Boquete, trail to lower edge of cloud forest, 5000–5800 ft, *Dwyer et al. 549* (MO). Cerro Punta, 2000 m, *Lao 348* (MO). Alto Quiel, Boquete, 2000 m, *Lao 356* (MO). Near El Boquete, 1000–1300 m, *Maxon 5379* (US). From Río Ladrillo to Alta de las Palmas, *Pittier 3268* (GH). Valley of the upper Río Chiriquí Viejo near Monte Lirio, 1300–1900 m, *Siebert 285* (MO). Finca Collins, near Boquete, 5800–6700 ft, *Stern et al. 2015, 2052* (both MO, US). Near Camesita, Volcán de Chiriquí, Boquete District, *Terry 1336* (A, MO). Opening to canyon to Bambito, 5000 ft, *Tyson 5864, 5866* (both MO). Llanos near Río Chiriquí Viejo Valley, *White 55* (GH, MO). Chiriquí Viejo Valley, *White 88* (GH, MO, US). Near El Volcán, *White 174* (GH, MO). Near Boquete, heavily forested slopes above the Río Caldera beyond Bajo Mono, 1800 m, *Wilbur et al. 11059* (MO). Near Vinca Lérida, 1750 m, *Woodson & Schery 221* (GH, MO). Potrero Muleto to summit, Volcán de

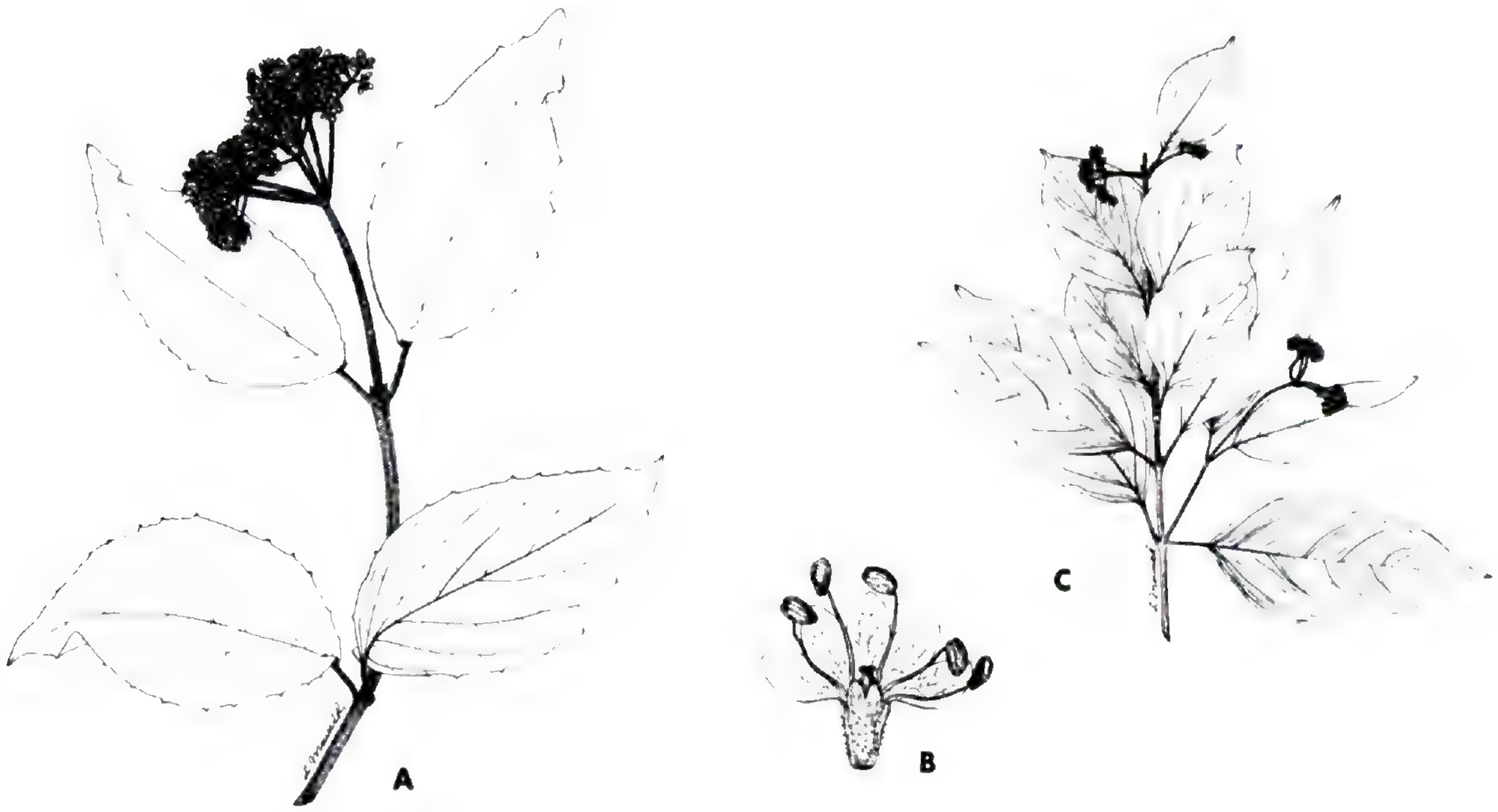

FIGURE 3. *Viburnum*.—A–B. *V. stellato-tomentosum* (Oerst.) Hemsl.—A. Habit (× 3⅓). —B. Flower (× 5).—[After *Stern et al. 1198* (MO).]—C. *V. costaricanum* (Oerst.) Hemsl., habit (× ⅓). [After *Dwyer 6966* (MO).]

Chiriquí, 3500–4000 m, *Woodson & Schery 390* (GH, MO, US). Near Casita Alto, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 794* (A, MO), *795* (A, MO). From Río Ladrillo to Alta de las Palmas, *Pittier 3268* (GH).

2. **Viburnum stellato-tomentosum** (Oerst.) Hemsl., Biol. Centr. Amer. Bot. 2: 3. 1881.—FIG. 3A–B.

Oreinotinus stellato-tomentosus Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1860: 83. 1861. TYPE: Volcán Irazú, Costa Rica, *Oersted 7818* (C, not seen).
Viburnum stellato-pilosum Polak., Linnaea 41: 564. 1877. TYPE: Volcán Barba, Costa Rica, *Polakowsky 349* (B, not seen; photo MO).

Shrub or *tree* to 8 m tall; branches terete, mostly glabrous and grey or reddish, dark, sometimes drying almost black, the twigs 6–20 cm long, densely tomentose with mostly sessile multangulate stellate hairs; bud scales tomentose but glabrescent. *Leaves* ovate, apically obtuse or acuminate, basally subcordate, rounded, or obtuse, often oblique, the margins entire or toothed, the teeth often appearing gland-tipped, above with dispersed to dense, sessile or stalked multangulate hairs and sparse, small, short-stalked glands, sometimes glabrescent, beneath densely tomentose, the midvein mostly recurved, the secondary veins 4–5 on each side, obscure near the leaf apex; petioles 5–15 mm long, tomentose; stipules absent. *Inflorescence* terminal, 2–4-times compound cymes 5–8 cm in diameter, the bracts narrow, spatulate to lanceolate, variable in size, to 5 cm long, the bracteoles linear, 2–5 mm long, rarely equaling the flowers, mostly pubescent; pedicels 1–2 mm long, tomentose. *Flowers* white, fragrant; calyx 2 mm long, the tube cylindrical or obconical, mostly with numerous stalked, red-dying glands, seldom glabrous or with eglandular simple hairs, the lobes deltoid to obtuse, sometimes emarginate, conspicuously ciliate, rarely pubescent dorsally; corolla campanulate, glabrate with a few hairs inside and out near the apex of the tube, 2–3 mm long, lobed to ca. ½ way down, the lobes rounded, quincuncial in bud; stamens exserted, the

filaments narrowed apically, slightly gibbous basally, the anthers ca. 1 mm long; the ovary 1-loculed, superior portion (style) conical, the stigmas 3, more or less distinct and unequal. *Fruit* an ellipsoid, black, juicy berry ca. 5 mm long.

This species may be recognised by its felty leaves which have conspicuous, small, ascending glandular-callose teeth, and by the even, stellate tomentum on the peduncles and pedicels. It is found at upper elevations in the Chiriquí mountains and in Costa Rica. Following his type description, Morton (1933) stated: "This, the commonest species of Costa Rica, is a round-topped tree with black edible fruit."

CHIRIQUÍ: Llanos del Volcán, 1300 m, *Allen 1538* (MO, NY, US). Llano del Volcán, 1500–1600 m, *Allen & Fairchild 3471* (MO, US). Elevated gravel benches 1 mi, SW of Boquete, 4000 ft, *Allen 4719* (MO, NY, US). Steep slope edge of cafetal, upper side of Boquete, *D'Arcy & D'Arcy 6478* (ADW, BIRM, C, CAL, COI, COL, CORD, DAO, DUKE, F, FSU, G, GH, K, L, LE, M, MO, MPU, NY, P, PMA, POM, PRE, T, TH, UCWI, US, VEN, WIS). Boquete, 3800 ft, *Davidson 620* (A, MO, US). Lava fields near town of Volcán, 4600 ft, *Duke 9141* (MO). Llanos del Volcán, 1120–1200 m, *Seibert 319* (MO). Llanos Francia near Boquete, 3300 ft, *Stern et al. 1198* (GH, MO, US). In deep arid canyon bottom 5 mi. NE of El Volcán, 6300–6500 ft, *Tyson 804* (MO). On old lava prairie 3 mi. N of El Volcán, 5000 ft, *Tyson 5719* (MO). Río Chiriquí Viejo Valley near El Volcán, *White 192* (GH, MO). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1103* (A, MO). El Hato de Volcán, llanos, *Ebinger 775* (US).

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Missouri Botanical Garden

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ANNALS OF THE
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ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

VOLUME 60
1973
NUMBER 2

ANNALS OF THE
Missouri Botanical Garden

THE THRUST OF PRESENT AND FUTURE RESEARCH IN THE LOWLAND TROPICS OF MEXICO[1]

Arturo Gómez-Pompa[2]

The subject I wish to discuss has worried me for many years, and even though I am still very far from having all of the facts and answers, I think I will take a chance and try to foresee the problematic near future of botanical research in the lowland tropics of Mexico.

I have found a similarity in the problems of obtaining scientific knowledge of tropical plants by non-resident botanists from extra tropical countries with the problems we have had in Mexico to develop botanical knowledge of tropical lowland areas by botanists resident in the highlands in Mexico City. It seems to me that the comparison is so close, that some of our thinking about this problem could be useful in other tropical areas as well.

I hope also that our experiences in Mexico can help to identify the same problems in other places and that we can make a joint effort to look for practical solutions.

My thoughts will be related mainly to botanical sciences (floristics and plant ecology) but may be appliable to other natural sciences as well.

The vegetation of the lowland tropical areas of the world is a very complex mosaic of communities composed by an endless combination of species. It is in these areas where we find the greatest terrestrial diversity of species and also the richest floras and faunas. It is also true that the biota of these areas is very poorly known. Often has been stated that the most important concepts in organismal biology will come from the study of tropical organisms. On the other hand we know that tropical species are the ones that are in more danger of extinction, because of the delicate and highly specialized life cycles of very many of them.

It is my intention on this occasion to give you my opinion on some of the reasons for having such a poor knowledge, some ways that this can be corrected, and the role that botanists can play in this regard. In Mexico we have a con-

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[1] From a talk given at the Nineteenth Annual Systematics Symposium, "Systematic Studies in the Lowland Tropics," Missouri Botanical Garden, 20–22 October 1972.

[2] Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

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siderable area of tropical lowlands, and the interest of our University in this region has been continuous for several decades since the pioneer work of Dr. Miranda and Prof. Matuda in southeastern Mexico. The rule of the poor knowledge of tropical lowland areas is still a valid one in Mexico, and a race against time is underway. The primary vegetation of these areas is being destroyed at a fantastic speed.

Why are these tropical lowland areas so problematic, and what can we do about it? I will try to answer these questions.

The first and most important answer is the almost total lack of development of botanical institutes in the tropical lowland areas.

Most of the botanists in the past and present are located in other regions. The reasons for this are complex; but, the result is that in the tropical lowlands of Mexico there were almost no botanical research centers, until very recently. No new local botanists were being trained, and even though there were persons interested in the lowlands, there was no future for them there, as there are no jobs available.

The general public is not aware of the importance of these types of activities and for that reason they do not care about them. There is almost no local support for research in these lines, and there are very few funds available for the very few persons interested in living and working there. I firmly believe that the lack of professionals living in these areas is one of the main reasons for the poor knowledge of the lowlands of the tropics, and this may be extended very well to other tropical areas of the world.

It seems to me obvious that any effort to create institutions for research in these areas should be encouraged, if these centers can open jobs for scientists who want to live and work there. It also seems evident to me that any research project that involves training of local personnel should also be encouraged.

Another great important problem of a different nature in these lowland areas is the scarcity of collections. If you followed some of the itineraries of many collectors in the past, they seem to stop at 800 m of altitude. There are several reasons for it; the difficulty of distinguishing one tree species from another, the difficulty of collecting specimens from a tree, liana, or epiphytes. In addition to this we have many other reasons: The unhospitable climate, mosquitoes, poisonous snakes, tropical diseases, and other reasons very well known in certain countries with political instability. In contrast with these facts we have the problems of the lack of interest for support of plant collectors in general in these areas. It has been stated that there are enough collections from tropical America already in herbaria which, if studied would give a good representation of the flora for these regions. As many of you know by personal experience, this is far from being the truth. As soon as you engage yourself in a study of a set of new collections from any lowland tropical area it is certain that you will find many new and interesting things.

The data from specimens from these areas are a good indicator of the poor knowledge of the regions and their environment. Data such as "in poor soils," "wet ravine," "shadowy places," "tropical jungle," etc. have very little meaning and reflect our poor knowledge of the areas and of the plants.

It is clear that the solution for this problem is rather simple: Promote scientific collecting activities in the lowland tropics as much as possible, and help any program that encourages this type of activity. A training period should be given to any person in order that they could provide good label data. It is surprising to know the number of scientific plant collectors that ignore the literature concerning the areas they are working.

Knowledge of the biology of tropical lowland plants in Mexico is almost nil, and the very little that is known has come mainly from sporadic visits of visiting botanists in a "hit or run" research basis. Of course the result is that there are so many superficial observations that one can hardly make use of them. There are very honorable exceptions, and it seems that in recent years this is changing rather rapidly for the better.

It is true that this lack of information of the biology of plants is rather general and extends to other regions and climates which also need to be studied. But I feel that there should be a high priority for tropical lowland plants, because of their diversity, their highly specialized life cycles, and the danger of their extinction.

How to solve this problem is more difficult because it involves more people, with different training and much more local facilities. So, there is a need to include in the curriculum for biologists a good deal of problem-oriented field research courses; also there is a need to have on-going research projects that may help to stimulate the interests of new researchers in this field. And also to provide local facilities to scientists in the lowland tropical areas so they can live comfortably for extended periods of time with the minimum difficulties.

Another related problem in the botanical research of tropical lowlands in Mexico is the incomplete information on the tropical environments. There are very few research programs on tropical soils and climate.

It is quite evident that very little can be done in botanical research without the help of other scientific disciplines. So, it is necessary, I think, to encourage interdisciplinary research projects. We cannot understand plant distribution without the aid of good geological, climatological, and edaphic maps. And the lives of plants can hardly be understood without the knowledge of their animal relationships. So, zoological and botanical research are very closely related in these regions.

Because of all these facts we can better understand why many of the floras, revisions, and monographs which include tropical lowland species are incomplete. We are still very far from understanding many of the species' relations and their variation in the lowland tropics. As more collections and data are accessible, many species described for incomplete materials fall into synonymy. As many revisions are based on few specimens per species (often only one), the results are obviously far from being precise.

In addition to all of these problems we have the most important of all, the alarming rate of destruction of the primary ecosystems with no hope for future regeneration.

The demand for new land in Mexico is so great that a large number of people are moving into the lowland tropical areas. And these are regarded as the

promised land of endless resources. The results are the explosive increase of agricultural and grazing land at the expense of the natural original ecosystems. Because of the lack of knowledge of these ecosystems their resources are destroyed without being used. Tropical forestry is still to be developed. In these areas there are almost no national parks or reserves and no active botanical gardens. So, there are almost no possibilities for conserving fragments of the natural ecosystems. In this race with time we know we started late, and it will be almost impossible to win; but we are trying. How?

We have tried to follow some of the solutions I just mentioned. Some of them are already been applied in our country, but many of them still need to be effected.

1. In the educational schemes at our University we are training new biologists with an awareness of the problem of tropical lands. Hundreds of students take our tropical biology field courses, and they become involved with short term research problems. A great number graduate and undergraduate students are getting trained in different fields of tropical botany, and it is my hope that they will provide the necessary critical number to have some influence in the whole country.

2. In our research projects in lowland areas we are planning to train personnel not only of our University but from local state universities as well. This will be done by scholarships, assistantships, and other means. We are completely aware that if we do not develop the local personnel, we will never go very far.

3. In the "Flora of Veracruz" program we are supporting scientific collecting activities in the areas by local personnel. And, we are planning that part of the collections remain in the local institution when appropriate personnel are available. This will help them obtain their own local support. We are going to encourage new botanists to go to centers in these areas and stay for longer periods of time. For this purpose we are expecting an increasing support from the government.

4. The new research institutions within the areas will need much support and for that reason we are promoting joint research programs with visiting professors, students, lectures, seminars, etc.

5. The gaps in knowledge and personnel are being filled by close cooperation with foreign institutions. Among them is our joint research project with Harvard for the "Flora of Veracruz" program which has the same basic objectives I have talked about: research and training.

Another action that has been taken is the acquisition of two biological reserves by our University, one in the Veracruz lowland humid region and the other in the Pacific Coast tropical lowland area. The new school of tropical Agriculture in Tabasco also has set apart a small rain forest reserve. These efforts are very small, but we hope that some response can come from other institutions with more power.

The last possible solution is to include applied aspects in any research program in which this could be done. We should emphasize the fact that tropical rain forests are very poorly used ecosystems. We do not know how to use their resources or how to regenerate them. It seems clear that the only way to protect these ecosystems is to know them and to know how to use them with conservation

methods. We should remember that we have to feed a rapidly growing population that will not stop to wait for us to study the rain forests.

From what I have said it seems there are a few suggesions that could be followed in general:

1. To include tropical biology problems in any biological curriculum.

2. To encourage plant collecting in the lowland tropics as much as possible before the plants have disappeared.

3. To promote joint research programs that include preparation of new personnel and especially those which include local persons.

4. To help local research institutions develop.

5. To create new research institutions in critical areas with a mixture of local and "foreign" staff.

6. To encourage funding institutions or associations to help finance local botanical research in the lowland tropics with no discrimination of nationality. It is rather sad to see how other sciences are being helped at an international level and no effort has been directed toward the botanical sciences, which should be the basis of development of higher priority. An International (Interamerican) Science Foundation is badly needed. Foreign aid agencies should invest in this line, which can be of greater and more effective impact.

7. To encourage research programs that can have some local application and to find ways to promote them.

To finish I would like to say that plant scientists cannot live in an ivory tower ignoring what is happening in the place they are working. The problems are larger than any national border, and to solve them there is a great need to remember that we have the obligation to make the general public know the importance of conserving the living plant resources of the world. Also we have an obligation with the society in which we live that exceeds geographical and institutional boundaries.

The future of botanical research on the tropical lowlands of Mexico seems to be very promising as many new young scientists are beginning to work in many different fields. What is not clear to me is the future of the primary vegetation still left in those areas. It is quite evident to me that secondary vegetation is taking over as it has happened in many other tropical areas and the consequences are not predictable. A new revolution in evolution is taking place and we are now merely unconscious spectators. I think the moment is here to study what is left, to conserve as much as we can at any cost, and to study the changes that are occurring. We should try to predict what will happen next in this new environment, and what are the evolutionary trends of the new secondary communities and species that are replacing the magnificent rain forests of the past. It may sound rather sad, but that is the way I see the future of most lowland tropical rain forests in Mexico, and probably this can also be applied in other countries as well.

STUDIES OF THE *PINUS RIGIDA-SEROTINA* COMPLEX I. A STUDY OF GEOGRAPHIC VARIATION[1]

PETER E. SMOUSE[2] AND LEROY C. SAYLOR[3]

ABSTRACT

Pinus rigida and *P. serotina*, two closely related taxa which inhabit the eastern United States, have been described historically as varieties and subspecies of *P. rigida* and as separate species. These taxa are allopatric except for a narrow contact zone coincident with the Delmarva Peninsula and southeastern New Jersey. In this contact zone intermediate specimens have been encountered, and these have been interpreted both as belonging to clinally intermediate populations of a single continuum and as natural hybrids between two sympatric taxa. The present study was undertaken to provide additional information about the relationship of *P. rigida* and *P. serotina* and the composition of populations in the contact zone.

A number of populations were sampled from the natural ranges of the two taxa and from the transition zone. Bud and seed characteristics, along with cone length, were found to be quite similar in the two taxa. Other features, such as needle length, peduncle length, cone diameter, and serotiny differed. All of these characters varied clinally within each taxon, and these clinal patterns converged toward the transition zone. The natural populations of this zone were shown to possess characteristics of a single taxon that were morphologically intermediate between nearby populations of the two taxa. They were interpreted as being intermediate populations of a single geographically variable complex. Evidence was detected of a local steepening of the morphological gradation through the transition zone, and this evidence was interpreted as supporting a system of secondary intergradation, rather than primary radiation.

The authors follow Clausen (1939) in denoting the taxa as subspecies: *P. rigida* subsp. *rigida* and *P. rigida* subsp. *serotina*, because they fail to maintain their separate morphological and reproductive integrities in the contact zone, where they coalesce into a single entity.

Pitch pine (*Pinus rigida* Mill.) and pond pine (*P. serotina* Michx.) are two closely related taxa of the genus *Pinus* L. subsection *Australes* Loud. which have long been the objects of taxonomic uncertainty. They have been described as distinct species (Shaw, 1914; Coker & Totten, 1945; Little, 1953), as varieties of *P. rigida* (Louden, 1838; Sargent, 1926; Sudworth, 1927; Harrar & Harrar, 1962), and as subspecies of *P. rigida* (Clausen, 1939).

The most commonly cited diagnostic features for these taxa are needle length, cone shape, size and persistence of prickles, and degree of cone serotiny. Clausen (1939) described a cline in needle length which extended from pitch pine in Massachusetts to pond pine in Florida and which passed through a limited contact zone coincident with the Delmarva Peninsula and southeastern New Jersey. He also observed that the size and persistence of prickles were quite variable within each taxon, and that serotiny was not entirely reliable as a

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[1] Paper number 3678 of the Journal Series of the North Carolina State University Agricultural Experiment Station, Raleigh, North Carolina, U.S.A. This study was supported, in part, by McIntire-Stennis funds (Project 4016) and by the National Aeronautics and Space Administration and the National Science Foundation, which provided fellowship support for the senior author.

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ANN. MISSOURI BOT. GARD. 60: 174–191. 1973.

diagnostic trait, being present in both taxa in areas with a prolonged fire history. Although Clausen interpreted the sympatric populations as clinal intermediates, Little *et al.* (1967) considered the intermediate specimens in the contact zone to be the result of natural hybridization between distinct taxa.

Interpretation of preliminary field observations of the present study agreed with the views of Clausen (1939), but the variation patterns encountered suggested that environmental factors other than latitude might play an important role in the variation observed. The presence of loblolly pine (*P. taeda* L.) in the contact zone complicated the issue, because natural hybridization of this species with *P. rigida* and *P. serotina*, as described by Little *et al.* (1967), was apparent. In addition, the possibility of hybridization with shortleaf pine (*P. echinata* Mill.) could not be ruled out. It became apparent, therefore, that a thorough field study would be necessary to resolve the situation. The present paper deals only with *P. rigida* and *P. serotina*, while the relationships and hybridization of these two taxa with *P. taeda* and *P. echinata* are covered in a subsequent paper (Smouse & Saylor, 1973).

The objectives of this study were: (1) to describe the variation which exists within and among populations of pond and pitch pines, exclusive of the transition zone, (2) to determine to what extent such variation is associated with major geographical and environmental factors, and (3) to determine whether the transitional populations consist of both taxa, both taxa and natural hybrids, or populations of a single taxon that follow a genetic and/or environmental continuum.

Sampling Procedure

A number of populations within and near the natural ranges of *Pinus rigida* and *P. serotina* and within the transitional zone between these taxa were chosen for study. Samples were obtained from a wide variety of geographical and environmental situations (Fig. 1). In and near the transition zone, populations were chosen for sympatry with *P. taeda* and/or *P. echinata*, but more distant population samples were only of a single taxon.

A sample of 15 trees was obtained from each of the taxa present at each location, if that many were available. Natural hybrids were also sampled wherever encountered. Details of the sampling procedures are given by Smouse (1970). Any tree suggestive of a hybrid combination involving either *Pinus taeda* or *P. echinata* was removed to avoid bias in the interpretation of the *P. rigida–P. serotina* analysis.

Trees were sampled for mature and yearling cones, foliage, and oleoresin. Collections for all but the oleoresin were restricted to the upper third of the crown whenever possible.

Within tree sampling involved 10 needle fascicles and 5 observations each for mature and yearling cones, dormant buds, and seeds. It was not always possible to obtain the desired numbers of observations for mature and yearling cones or dormant buds, however, so unweighted tree means were used for all analyses. Nine morphological characters were finally chosen for examination. Only trees with a complete set of nine character values were used in analysis.

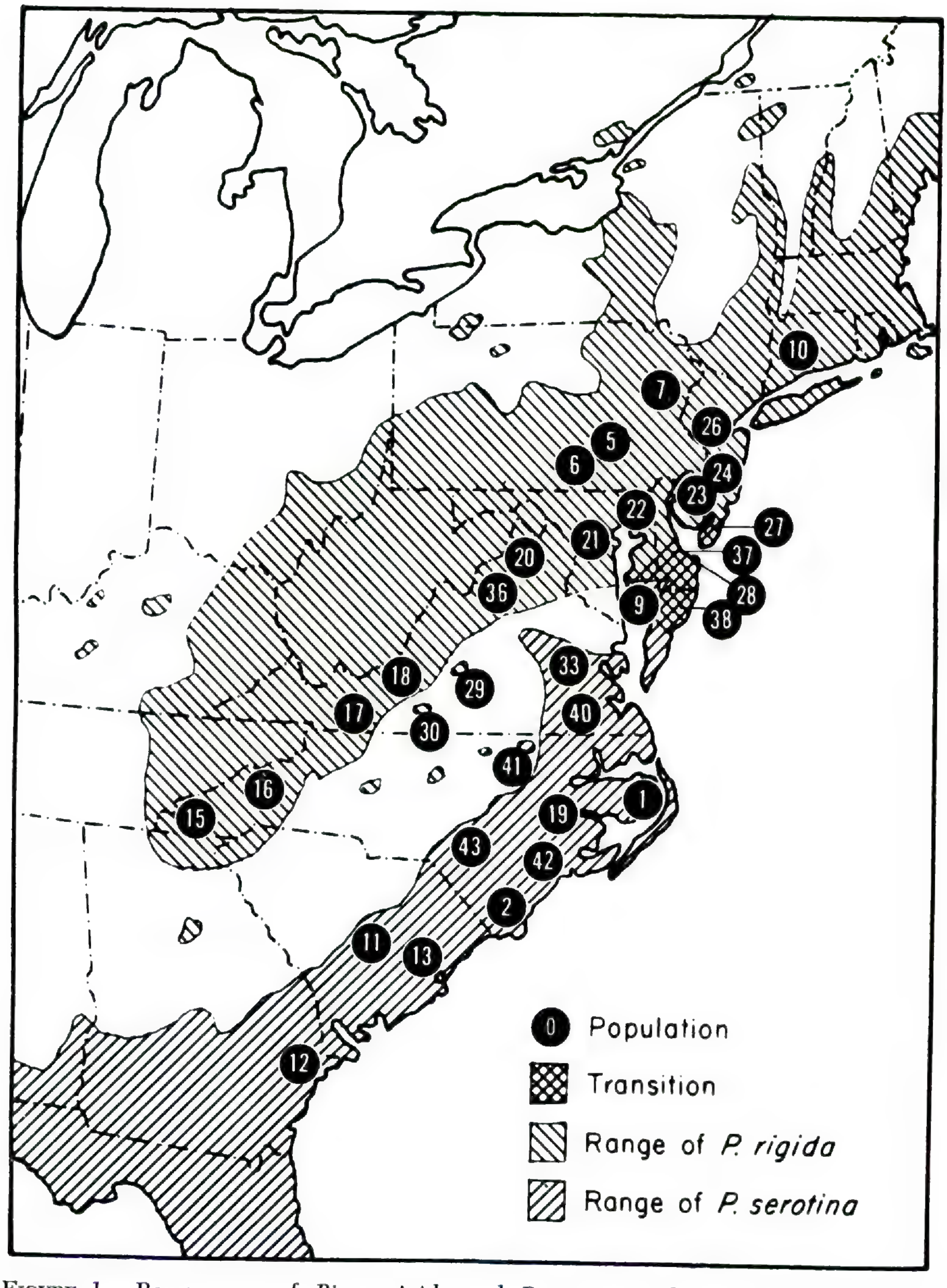

FIGURE 1. Range map of *Pinus rigida* and *P. serotina*, showing locations of sample populations.

ANALYSIS AND RESULTS

Statistical Strategy: To achieve all three objectives with any precision it was necessary to develop a unified statistical approach. Two different interpretations of the transitional populations were posed as alternative hypotheses. The first hypothesis was that each of the transitional populations represented a clinally intermediate population between the two extremes of a genetic continuum. The second hypothesis was that each of these populations consisted of two taxa

(pitch and pond pines), possibly with hybrids. To distinguish between these alternatives it was necessary to: (1) detect and measure the variation within each taxon, while ignoring the transitional populations, (2) construct an abstract picture (standard image) of each of the taxa at each location of the transitional populations, and (3) compare each transitional specimen with the images of the two taxa.

If the transitional specimens consisted of a mixture of both taxa (with or without hybrids), their distribution should be distinctly bimodal, and the variance within the mixture should greatly exceed that within either taxonomic standard. If the transitional specimens consisted of a single taxon, then the distribution should be unimodal, and the variation within the transitional type should be comparable to that within each of the taxonomic standards.

Geographic Variation: Mean values for each of the morphological characters differed among locations; in addition, there was considerable variation within populations (Table 1). Cone serotiny was difficult to quantify, so a subjective scoring procedure was devised; this was based upon the maximum number of years that cones remained closed on a given tree (Table 2).

Differences between the taxa were small (relative to the variation within taxa) for fascicle sheath diameter, cone length, seed thickness, and seed wing length. Differences for needle length, peduncle length, cone width, cone shape index, and serotiny score were more pronounced, although the ranges of variation within the taxa overlapped somewhat. An examination of Tables 1 and 2, along with Figure 1, reveals a tendency for decreasing needle length and peduncle length with increasing latitude within both taxa. The same characters increase in value with elevation in *Pinus rigida*, but since elevation and latitude are inversely correlated for *P. rigida*, it is not possible to clearly separate the elevational from the latitudinal associations. Cone width tends to decrease toward the transition zone in both taxa, while cone shape index increases toward the transition zone.

Precise measurement of clinal variation is a problem in regression analysis. The use of multiple regression for the description of geographic variation in a single character is a well known technique. Details of the type of multivariate regression anlaysis employed for the description of geographic variation in the present study are given by Smouse (1970).

The method results in a set of regression equations which describe variation in each of the characters as a linear function of four environmental variables: logarithm of latitude (X-1); logarithm of elevation (X-2); potential solar radiation (X-3)[4]; and a measure of site productivity (X-4). These environmental measures were intended only as rough indices for the various habitats. To the extent that they described the totality of associated environmental features of importance (*e.g.* rainfall and temperature regimes, photoperiodic phenomena, and general site fertility), they were expected to be useful for interpretation of the pattern of morphological variation encountered in the field.

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[4] Defined as total potential incident solar beam irradiation per annum, measured in hundreds of Langleys (kg-cal/cm^2), and tabulated by Frank and Lee (1966).

TABLE 1. Population means and variances for eight taxonomic traits of *Pinus rigida*, *P. serotina*, and transitional populations.

Population (number)	Trait[a]							
	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7	Y_8
Pinus rigida								
(15)	135(179)	231(738)	8(1)	61(62)	36(3)	25(4)	197(135)	170(367)
(16)	119(363)	222(281)	8(8)	59(65)	36(11)	22(8)	184(211)	164(176)
(17)	124(339)	255(1014)	6(6)	55(38)	35(6)	20(7)	180(425)	161(245)
(30)	134(303)	239(807)	9(14)	62(62)	39(15)	23(11)	178(198)	158(205)
(29)	105(0)	247(924)	9(0)	69(12)	41(1)	25(0)	193(9)	168(60)
(18)	113(74)	230(304)	8(3)	56(33)	34(6)	22(8)	173(462)	168(234)
(36)	135(89)	249(688)	10(6)	55(62)	35(10)	21(6)	173(128)	156(120)
(20)	132(29)	243(187)	7(4)	56(48)	36(15)	21(9)	188(129)	158(312)
(21)	129(431)	239(187)	8(7)	57(30)	35(9)	22(11)	176(211)	165(373)
(23)	103(131)	216(253)	3(1)	58(25)	35(7)	22(8)	158(209)	165(120)
(22)	116(140)	236(407)	7(3)	56(23)	33(5)	21(4)	162(181)	169(177)
(06)	80(42)	222(279)	5(4)	53(41)	33(7)	20(5)	175(131)	162(84)
(24)	111(92)	217(278)	4(4)	54(25)	34(11)	22(3)	155(145)	163(200)
(26)	119(222)	233(374)	7(13)	62(48)	37(15)	23(13)	167(149)	168(70)
(05)	111(120)	227(140)	5(2)	55(38)	33(8)	19(6)	172(120)	167(276)
(07)	105(173)	219(281)	4(3)	51(62)	31(15)	18(3)	176(253)	162(124)
(10)	100(315)	234(131)	5(1)	49(123)	31(21)	20(6)	174(105)	154(263)
Transitional Populations								
(38)	148(533)	237(268)	8(5)	56(24)	34(6)	21(7)	153(163)	163(200)
(09)	156(–)	259(–)	13(–)	64(–)	36(–)	25(–)	155(–)	175(–)
(37)	151(383)	239(464)	8(6)	61(41)	38(12)	22(3)	170(211)	163(173)
(28)	133(125)	250(160)	9(4)	67(35)	39(13)	23(5)	177(291)	170(128)
(27)	129(181)	230(270)	5(8)	66(31)	40(14)	24(5)	165(169)	168(215)

[a] The taxonomic traits are:
Y_1 = Needle length (mm)
Y_2 = Sheath diameter (.01 mm)
Y_3 = Peduncle length (mm)
Y_4 = Cone length (mm)
Y_5 = Cone width (mm)
Y_6 = Seed wing length (mm)
Y_7 = Seed thickness (.01 mm)
Y_8 = Cone length/cone width
A(B): A = Population mean; B = Population variance

TABLE 1. (Continued)

Population (number)	Trait[a]							
	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7	Y_8
Pinus serotina								
(12)	211(226)	270(485)	13(9)	58(101)	38(10)	20(12)	161(155)	154(306)
(13)	198(459)	240(186)	11(8)	58(37)	39(16)	21(8)	164(52)	147(117)
(11)	211(509)	249(358)	12(9)	60(25)	40(14)	24(6)	167(115)	148(63)
(02)	170(294)	244(306)	11(6)	51(11)	34(5)	29(2)	155(115)	149(153)
(42)	189(623)	246(761)	12(13)	56(19)	41(12)	22(7)	158(262)	137(39)
(19)	169(562)	239(394)	10(16)	61(68)	40(25)	22(11)	161(272)	149(130)
(43)	185(371)	251(373)	11(11)	66(55)	44(24)	25(14)	172(255)	139(160)
(01)	190(233)	251(689)	11(11)	62(33)	43(12)	21(5)	168(218)	143(135)
(41)	154(662)	231(961)	9(5)	67(7)	48(16)	27(1)	181(457)	139(91)
(40)	183(239)	256(143)	14(11)	58(16)	40(9)	22(7)	171(318)	144(75)
(33)	167(492)	248(618)	10(6)	60(99)	37(24)	22(15)	158(73)	160(196)

TABLE 2. Degree of cone serotiny (populations arranged by increasing latitude).

Population	Number of Trees Score[a] 1	3	5	Average value	Population	Number of trees Score[a] 1	3	5	Average value
Pinus rigida					*Pinus serotina*				
(15)	9	0	0	1.00	(12)	0	2	7	4.56
(16)	10	0	0	1.00	(13)	0	9	4	3.62
(17)	12	0	0	1.00	(11)	0	6	6	4.00
(30)	12	0	0	1.00	(02)	0	0	9	5.00
(29)	2	0	0	1.00	(42)	0	0	11	5.00
(18)	9	0	0	1.00	(19)	0	0	12	5.00
(36)	12	0	2	1.57	(43)	6	2	4	2.67
(20)	10	0	0	1.00	(01)	0	0	16	5.00
(21)	12	0	0	1.00	(41)	1	0	2	3.67
(23)	14	0	0	1.00	(40)	7	4	4	2.60
(22)	18	0	0	1.00	(33)	4	4	8	3.50
(06)	12	0	0	1.00	Transitional Populations				
(24)	4	5	2	2.64	(38)	15	0	1	1.27
(26)	6	6	1	2.23	(09)	1	0	0	1.00
(05)	11	0	0	1.00	(37)	15	1	0	1.12
(07)	10	0	0	1.00	(28)	16	6	3	1.96
(10)	4	0	0	1.00	(27)	15	4	4	2.17

[a] Scoring system:
1 = Not serotinous.
3 = Maximum serotiny no more than one year.
5 = Maximum serotiny more than one year.

Two of the nine characters were removed from the analyses, because they were statistically objectionable. The serotiny index was not a continuous variable and was too crudely scored to justify its inclusion in a sensitive statistical analysis. Cone length-width ratio was also removed for reasons given below. The statistical analyses employed in the study assumed a normal distribution for each character. Both cone lengths and cone widths were symmetrically distributed and were close to being normally distributed. These characters were strongly correlated, which accounts for the utility of the shape index. The ratios of two normally distributed variables are not normally distributed, however, and when a high correlation exists between the components, the distribution is not necessarily even symmetrical. In the present instance symmetry was considered the more desirable property, because of the necessity of projecting taxa to new locations. A careful preliminary check also indicated that the ratio provided no information that could not be obtained from cone length and width jointly. Consequently, the shape index was dropped.

Using multivariate test procedures, it was determined that the association between morphological and environmental variation was very highly significant within each of the two taxa. However, the multivariate test is for composite association and must be broken into the univariate (single character) components for detailed analyses. This was easily accomplished, since the regression equation for each single character was the same as that which would have resulted from a univariate multiple regression analysis. Each character was separately subjected to an analysis of covariance, as shown in Table 3. No attempt was made

TABLE 3. Analysis of covariance form.

Source of variation	Degrees of freedom	Sums of squares	Mean squares	F tests
Pinus rigida				
Among populations	16	$S_1 = S_2 + S_3$	$M_1 = S_1/16$	$M_1/M_4 = F_{16,166}$
Regression	4	S_2	$M_2 = S_2/4$	$M_2/M_4 = F_{4,166}$
Lack of fit	12	S_3	$M_3 = S_3/12$	$M_3/M_4 = F_{12,166}$
Within populations	166	S_4	$M_4 = S_4/166$	
Pinus serotina				
Among populations	10	$S_1 = S_2 + S_3$	$M_1 = S_1/10$	$M_1/M_4 = F_{10,117}$
Regression	4	S_2	$M_2 = S_2/4$	$M_2/M_4 = F_{4,117}$
Lack of fit	6	S_3	$M_3 = S_3/6$	$M_3/M_4 = F_{6,117}$
Within populations	117	S_4	$M_4 = S_4/117$	

to separate the contributions of the four environmental factors, since these factors were rather highly correlated. The lack of fit term, a measure of the failure to describe completely the morphological differences among populations by the four environmental indices, was estimated separately from the within population variation.

Population differences were large for all characters in *Pinus rigida*, and the environmental covariates were collectively effective in describing this variation for all characters except cone length (Table 4). The lack of fit terms were also generally large, indicating the presence of still "unexplained" geographical variation.

Population differences were evident within *Pinus serotina* for needle length, cone length, closed cone diameter, and seed wing length. The regression analyses were quite effective for needle length and cone diameter but were less so for cone length and seed wing length. Significant lack of fit was likewise evident for needle length and cone diameter. Although the lack of fit for all

TABLE 4. F-Values for tests of differences among populations, for utility of regression and for lack of fit.

Source of variation	Character[a]						
	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
Pinus rigida							
Among populations	13.08*	3.68*	7.27*	3.08*	4.90*	3.89*	6.18*
Regression	26.09*	6.09*	12.76*	4.14	8.32*	9.36*	18.23*
Lack of fit	8.87*	2.87*	5.44*	2.72*	3.75*	2.07	2.16
Pinus serotina							
Among populations	7.51*	1.88	2.23	3.64*	7.35*	3.25*	2.43
Regression	9.50*	.28	.93	4.46	7.52*	5.35	.91
Lack of fit	6.18*	2.94	3.09	3.10	7.24*	1.85	3.43

[a] The characters are:
Y_1 = Needle length (mm)
Y_2 = Fascicle sheath diameter (.01 mm)
Y_3 = Peduncle length (mm)
Y_4 = Cone length (mm)
Y_5 = Closed cone diameter (mm)
Y_6 = Seed wing length (mm)
Y_7 = Seed thickness (.01 mm)
* = Significant at the 5% level

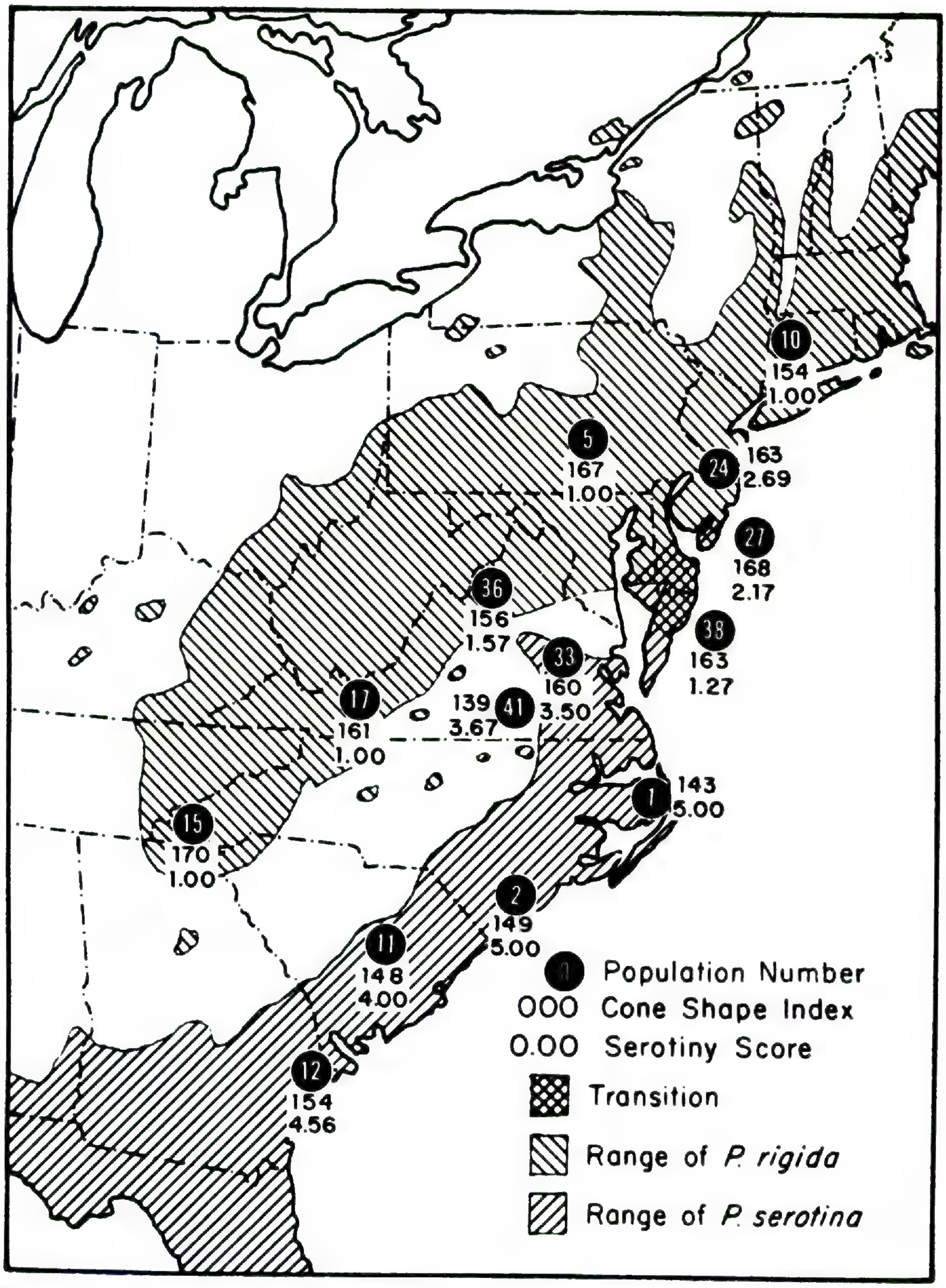

FIGURE 2. Range map of *Pinus rigida* and *P. serotina*, showing cone shape index and serotiny score for selected populations.

characters in both taxa was an appreciable portion of the total variation among populations, the regression mean squares (and F values) were generally larger than those for lack of fit, and the attempt to associate morphological and environmental variation was judged to be a general success.

Serotiny score and cone shape index were not subjected to statistical analysis, but a general picture of their respective variation patterns can be obtained from Figure 2. Serotiny score shows a clear geographic pattern. The closed cone

habit in *Pinus rigida* is lacking except in two areas represented by populations 24 and 36; both of these are near the range of *P. serotina*. Serotiny varies in *P. serotina*, decreasing as one moves northward and up onto the piedmont. It is interesting that the serotiny scores of populations 27 and 38 are less than that of population 24. Ledig[5] (personal communication) has shown that serotiny in *P. rigida* is most prevalent in the Pine Barrens of New Jersey, and decreases in all directions away from that area. Whether this pattern represents past influence from *P. serotina* or locally severe selective pressures, it is clear that the transitional populations are intermediate between the two taxa for this character. Cone shape index values are not intermediate for the transitional populations, being larger than is usual within either taxon. This seems to be the result of tendencies for increasing cone length and decreasing cone diameter near the transition zone within both taxa.

Several other characters not included in the analyses warrant some attention. The size and shape of cone prickles were not scored in this study, because preliminary observations indicated that the pattern of variation paralleled that of serotiny, *i.e.* the greater the degree of serotiny, the less evident the prickles. Specimens of yearling cones and dormant buds were not available in sufficient quantities to include in the analyses, but it was clear that conelets and buds were almost indistinguishable for the two taxa.

Limited data have been published on the oleoresin composition of these two taxa, which would indicate that the taxa differ qualitatively in composition of the monoterpene fraction of the oleoresin. *Pinus rigida* was found on at least one occasion (Hamrick, personal communication)[6] to contain appreciable quantities of β-Phellandrene, while *P. serotina* has been characterized as having large quantities of *l*-Limonene (Mirov, 1961). Our own analyses are not complete, but preliminary observations indicate that separation of these two taxa on only qualitative differences may not be possible. About half of the *P. rigida* trees examined to date possessed neither β-Phellandrene nor *l*-Limonene in appreciable quantities, whereas over half of the *P. serotina* trees examined were found to possess β-Phellandrene rather than *l*-Limonene.

In view of the claim that these two taxa grade together clinally, it is of considerable interest to obtain an overview of the pattern of the variation. A separate description of all characteristics is precluded by limitations of space. The general pattern of clinal variation found within each taxon indicated that the two taxa are much more similar near the transition zone than farther away. The overall morphological pattern was rather striking, as can be seen in Figure 3, which was constructed as follows. A discriminant function was computed from the taxon means and the residual covariance matrices. A com-

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[6] Unpublished internal report by J. L. Hamrick, Institute of Forest Genetics, Placerville, California.

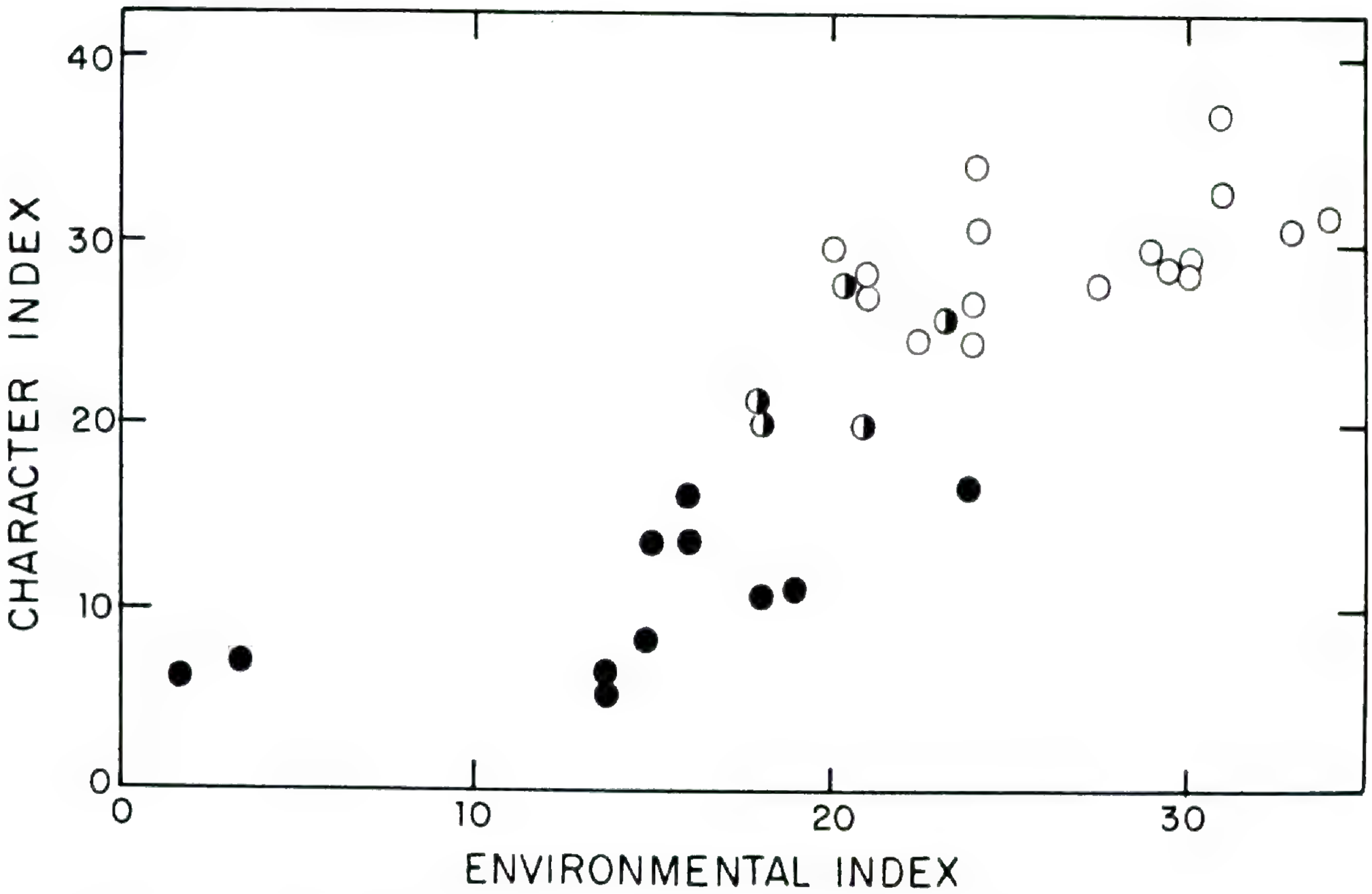

FIGURE 3. Variation of a morphological character index among populations of *P. rigida*, open circle; *P. serotina*, closed circle; and the transitional type, half-closed circle, in relation to an environmental index.

bination character index was then obtained by scoring each tree according to equation (1):

$$Y^* = a_1Y_1 + a_2Y_2 + \ldots + a_7Y_7, \quad (1)$$

where the a's are the character weights derived from the discriminant analysis. Next, an average regression equation was obtained for each character by averaging the separate equations for the two taxa. A combination environmental index was then constructed by subjecting the regression equations to the same set of weights as the morphological characters. The character index was then plotted against the environmental index (Fig. 3) in an effort to portray graphically the clinal patterns within and between these taxa. The picture is one of two clinally varying taxa connected by a series of intermediate or transitional populations. It is clear that there is no discontinuity, but the gradient does steepen in the transition area.

Although Figure 3 suggests that the transitional populations may consist of a single clinally intermediate type, it is not in itself conclusive. The average of two distinct taxa at these locations might well yield a similar result. In addition, Figure 3 shows an average environmental trend for the two taxa and an average morphological appearance. To provide a more rigorous evaluation, a separate comparison was made of each transitional specimen with each of the taxa as these taxa would appear if they actually existed in the transitional area.

Construction of Taxonomic Images: To determine the likely appearance of each taxon at each of the transitional locations (without reference to the speci-

TABLE 5. Means and variance of projected *Pinus rigida* and *P. serotina* and of the transitional populations.

Population	Taxon	Character[a]						
		Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
——	*P. rigida* (Unadjusted species means)	117(286)	233(454)	7(7)	57(49)	35(11)	21(7)	174(214)
(09)	*P. rigida* (Adjusted)	140(313)	239(498)	8(8)	61(54)	38(12)	25(8)	160(234)
	Transitional	156(–)	259(–)	13(–)	64(–)	36(–)	25(–)	155(–)
	P. serotina (Adjusted)	161(579)	241(557)	9(13)	68(58)	46(23)	24(10)	169(243)
(27)	*P. rigida* (Adjusted)	127(300)	232(478)	7(7)	59(52)	36(12)	24(8)	159(225)
	Transitional	129(181)	230(270)	5(8)	66(31)	40(14)	24(5)	165(169)
	P. serotina (Adjusted)	142(722)	230(695)	7(16)	77(72)	55(29)	27(13)	176(303)
(28)	*P. rigida* (Adjusted)	124(321)	239(511)	6(8)	61(55)	37(13)	25(8)	150(241)
	Transitional	133(125)	250(160)	9(4)	67(35)	39(13)	23(5)	177(291)
	P serotina (Adjusted)	159(554)	239(532)	10(12)	62(56)	43(22)	22(10)	166(232)
(37)	*P. rigida* (Adjusted)	141(307)	239(488)	8(7)	59(53)	37(12)	24(8)	168(230)
	Transitional	151(383)	239(464)	8(6)	61(41)	38(12)	22(3)	170(211)
	P. serotina (Adjusted)	168(544)	250(532)	11(12)	63(55)	41(22)	23(10)	168(228)
(38)	*P. rigida* (Adjusted)	139(296)	239(471)	7(7)	59(51)	37(12)	24(8)	166(222)
	Transitional	148(533)	237(268)	8(5)	56(24)	34(6)	21(7)	153(163)
	P. serotina (Adjusted)	167(529)	247(509)	11(11)	62(53)	41(21)	23(10)	169(222)
——	*P. serotina* (Unadjusted species means)	187(507)	248(487)	11(11)	60(51)	41(20)	23(9)	165(212)

[a] The characters are:
Y_1 = Needle length (mm)
Y_2 = Sheath diameter (.01 mm)
Y_3 = Peduncle length (mm)
Y_4 = Cone length (mm)
Y_5 = Cone width (mm)
Y_6 = Seed wing length (mm)
Y_7 = Seed thickness (.01 mm)
A(B): A = Mean; (B) = Variance.

mens actually obtained at these locations), an abstract standard was constructed for each taxon by extrapolative regression procedures. Each standard consisted of an estimated array of seven character means and a corresponding covariance matrix. The details of this procedure are to be found in Smouse (1970), but it is worth noting that the covariance matrix in question was the residual covariance matrix. This matrix included both the within population variation and the lack of fit variation, and served as a conservative estimate of all variation within a taxon (after removal of the clinal variation). The estimated means and variances of the seven characters are listed for each taxonomic standard and each transitional population in Table 5. All further references to the two taxa at the transitional locations should be understood to refer to the abstractions constructed as indicated above.

It can be seen from these data that for transitional locations, except location 27, the means of the estimated standards of the two taxa are more similar than the comparable means for the unadjusted averages of these same taxa. This general morphological convergence of the taxa in the transitional locations is not surprising in view of the patterns exhibited in Figure 3. This indicates the necessity of allowing for geographically associated morphological variation when contrasting the two taxa.

In spite of the similiarity of the two taxonomic standards, however, the character means of the transitional populations are not all intermediate between the appropriate mean values for the taxa. Two factors should be considered. First, the projections are subject to estimation errors. This is particularly true since the responses of the taxa to environmental variation at the edges of their respective ranges may not be strictly linear, as are the projections. Second, most of the actual values obtained for the transitional locations deviate from the average of the two images no more than the means of environmentally similar populations within each taxon deviate from each other. Each of the transitional population mean values is well within the range of variation of either taxonomic standard appropriate for the location in question. Thus, it appears that each of the transitional populations represents some sort of average between the two taxa.

The projected means of *Pinus serotina* at location 27 appear to be suspect. Cone length (Y_4) and cone width (Y_5) are particularly conspicuous by their deviations from other *P. serotina* mean values. Such deviations might be a reflection of two situations. The location in question is well outside the sampled range of *P. serotina*, and it is possible the values presented are a good reflection of what *P. serotina* really would look like if it were growing at that location. Alternatively, it is possible that estimation errors are involved in the considerable environmental extrapolation necessary to construct the standard. It is not possible to determine which condition is the more likely cause of these extreme values. In any event, the standard is the best available from the data at hand.

Discriminant Analysis: The next step in the analysis was to construct a discriminant function of the form shown in equation (1) for each of the transitional locations. Since the means and covariance matrices were different at each location, the resulting functions were also different. By arbitrarily scaling the

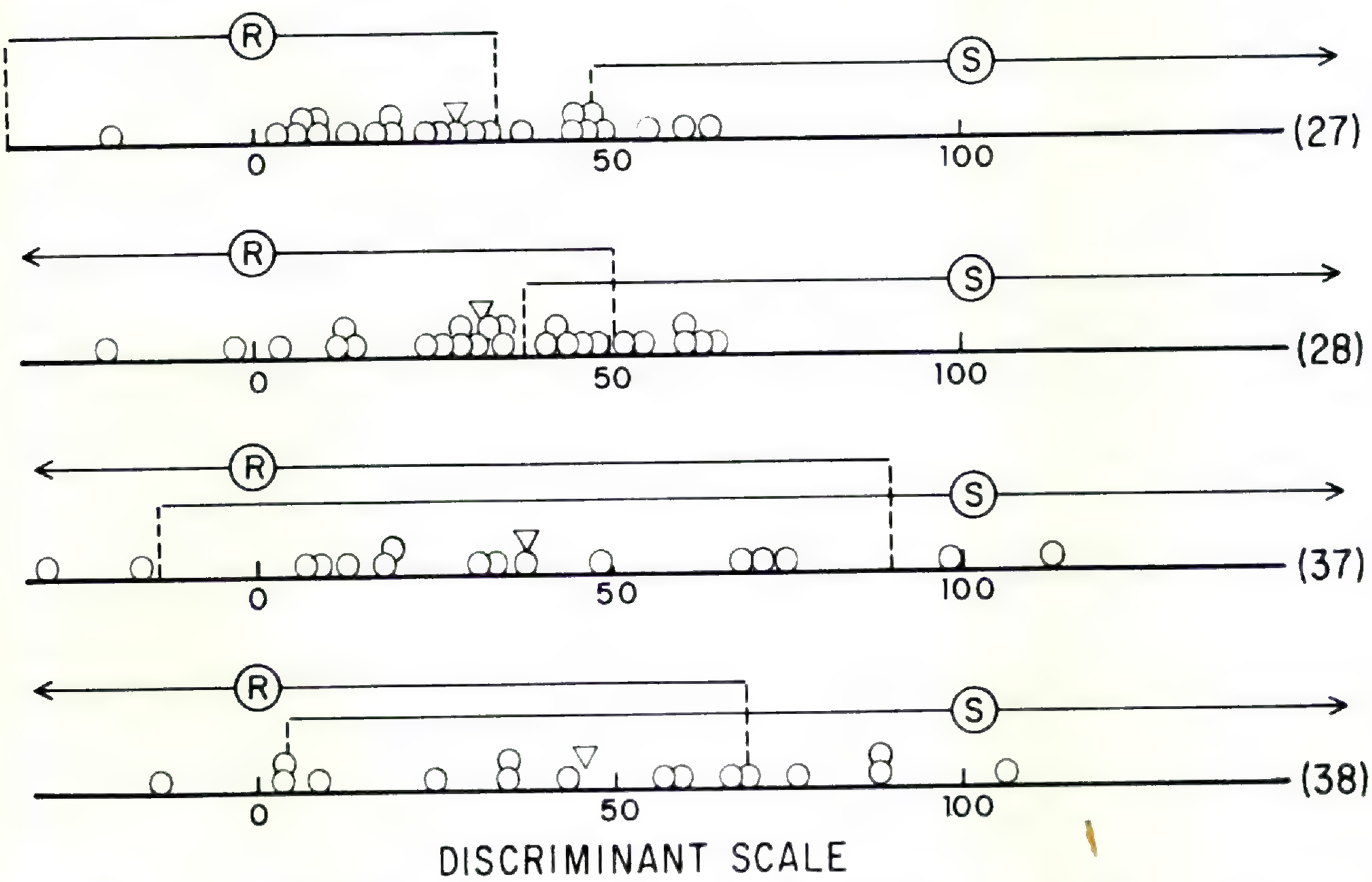

FIGURE 4. Discriminant analysis of transitional populations 27, 28, 37, and 38. Circled-R, mean and 95% confidence interval for *Pinus rigida*; circled-S, mean and 95% confidence interval for *P. serotina*; inverted triangle, mean of transitional population; open circle, discriminant score of a transitional specimen.

differences between the taxa to a constant, however, it was possible to compare the transitional locations (Fig. 4). Because population 09 was represented by only a single specimen, it is not shown. The theoretical 95% confidence intervals were computed by standard techniques.

Considerable overlap of the taxonomic standards at locations 37 and 38 is evident, even though the discriminant function maximizes the resolution of the taxa. The two taxonomic standards are more distinct at locations 27 and 28. There are too few specimens available at any of these locations to determine whether or not the variation was bimodal, but the variance within each of the transitional populations was quite comparable with that within either taxonomic standard. This observation supports the single taxon hypothesis.

Determination of whether one or a mixture of taxa exist in the transitional area can be approached in still another way. If both *Pinus rigida* and *P. serotina* were present in each of the transitional populations, then about half of the unidentified *P. rigida* specimens should have index values below the estimated mean of *P. rigida*, and about half above. A similar situation should also exist for the unidentified *P. serotina* individuals. This symmetry about the mean follows from the normality of the various characters, both individually and in linear combination. If we ignore the single specimen from population 09, we have only 8 out of 81 unidentified specimens falling either below the mean of *P. rigida* or above that of *P. serotina*. This would be a very unlikely result if two taxa were present.

It is possible that some of these 81 specimens are hybrids, and hybrids would

naturally fall between the taxa. Since this would lead to an overestimate of the number of species specimens between the taxonomic means, the hybrids should not be counted. Therefore, for the sake of argument, we might conservatively assume that no more than 40 of these 81 specimens represent one or the other taxon; for simplicity we might assume 20 specimens of each taxon. We should then expect about 20 values to fall between the means and about the same number to fall to one side or the other. The probability of obtaining as many as 32 between the means and as few as 8 to the outside is still negligibly small. There is no particular reason to assume equal numbers of the two taxa or that as many as 40 of the specimens belong to one or the other of the taxa, but the argument is sufficient to illustrate the point. It appears that the transitional populations represent clinally intermediate populations between the two extremes of a single genetic and/or environmental continuum.

DISCUSSION AND CONCLUSIONS

Serious discriminatory difficulties between the taxa actually arose in two zones. The first was the aforementioned transition zone. The second was a zone between populations 33 and 36, to the north and west of Richmond, Virginia. The two taxa are geographically close in this area (Fig. 1), and intermediate specimens were occasionally encountered. It may well be that this area either is or has been a second transition zone. This possibility is supported by the fact that population 33 is suggestive of *Pinus rigida* in many respects, while population 36 is equally suggestive of *P. serotina*.

The local steepness of the shift in these two zones could be used to support either of two hypotheses. The first is that the rapid morphological shift simply reflects a local steepening in an underlying selective gradient upon a series of populations which arose by adaptive radiation. The second is that this morphological gradation has resulted from secondary intergradation of two closely related taxa, rather than from primary radiation. No conclusive data are available to resolve this question, but the authors are more inclined to the second view.

Considerable evidence (Whitehead, 1965) is now available to indicate that the vegetation considerably to the south of the present transition zone was more boreal during maximum Wisconsin glaciation than at present, indicating a corresponding southward displacement of the more austral flora to which both of these taxa belong. The advance of glaciation provides a likely mechanism for inducing southward movement of a single taxon and geographic separation into two parts. Northward movement of both entities subsequent to glacial retreat could have resulted in sympatry in or near the present zone. The process of geographic isolation, adaptive radiation, and subsequent secondary intergradation need not have been completed in a single glacial cycle, there being four such periods in the Pleistocene.

The secondary intergradation hypothesis assumes that the two taxa are capable of hybridization. Artificial hybridization of these two taxa has demonstrated that crossability is very high (Smouse, 1970), but the lack of increased variation in the transition populations indicates that any excessive genetic segrega-

tion which might have followed such hybridization has been eliminated, probably by selection. As a result, a series of locally adapted, clinally intermediate populations now exist.

It is conceivable that hybridization of *Pinus rigida*, *P. serotina*, or their transitional type with one or more other taxa (*e.g. P. taeda*) may be the cause of some of the variation patterns encountered (*e.g.* for cone shape), particularly in the transition zone. While every effort was made to remove the influence of other taxa from the samples used here, it should be pointed out that the whole complex hybridizes naturally with *P. taeda*. Past influence of *P. taeda* on *P. serotina* was particularly evident in populations 41 and 43, but the infiltration appeared to be of such a long standing nature and so pervasive that removing this influence from *P. serotina* was not possible.

The primary objective of this study, specifically to describe the relationship of the transitional populations to both pond and pitch pines, was accomplished with new levels of precision. However, this in turn revived the problem related to classification of the various components of the *P. rigida-P. serotina* complex. Problems associated with determining taxonomic status have been well documented (*e.g.* Grant, 1963; Mettler & Gregg, 1969). These are related primarily to the question of how much morphological and/or reproductive differentiation is required before a pair of taxa should be considered separate species. Although criteria that can be objectively and practically applied are difficult to define, much of the controversy (*i.e.* taxonomic *vs.* biological species) can be avoided, if for a particular case, the criteria used for judgment are clearly stated.

As explained by Mettler and Gregg (1969), the term species is used in two ways: (1) as a taxonomic designation of organisms that are morphologically distinct, and (2) as a designation of entities which constitute reproductively isolated breeding populations. The first use is more convenient for cataloging, while the second is used more to reflect evolutionary relationships and restrictions of gene exchange. In the latter case, although ascertaining morphological differences is still quite necessary, the reproductive relationship among populations is considered more important than morphological differences between individuals. The test of sympatry, *i.e.* ability to maintain distinctness when coexisting in the same habitat, is of paramount importance. The types of classification dictated by these two points of view are not always compatible, and rather than adopt one or the other, the authors prefer to adopt a middle course.

It is common in plant taxonomy to employ varietal status for taxa which show minor morphological differences; generally, statistical differences exist in average appearance, but considerable overlap occurs among individual specimens. Reproductive barriers among varieties are generally lacking, and genetic exchange is quite easy, given the opportunity. Subspecies are usually more distinct morphologically, and reproductive barriers are greater than for varieties, although not absolute. Subspecies generally cannot withstand the test of sympatry, in spite of these barriers, and coalesce both genetically and morphologically where they come into contact. Species status is usually reserved for taxa which are clearly distinct morphologically and which are known or assumed

to be capable of withstanding the test of sympatry. Reproductive barriers need not be absolute, but the taxa should maintain their basic genetic and morphological integrity in sympatry, in spite of limited genetic exchange.

On the basis of the above criteria, the authors do not feel that separate specific status is warranted for pitch and pond pines for the following reasons. (1) In the only areas these two taxa are found together, they fail the test of sympatry. (2) As a complex, pitch and pond pines hybridize relatively freely with *Pinus taeda*, and with *P. echinata* to a slightly lesser degree. (3) All three entities (*P. rigida-serotina* complex, *P. taeda* and *P. echinata*) maintain their separate genetic and morphological integreties in sympatric populations in spite of the ability to hybridize.

Varietal status does not appear appropriate either. The morphological differences between *Pinus rigida* and *P. serotina*, taken as a whole, are not minor, in spite of clinal integradation through the transition zone. The steepeness of the transitional gradient serves to connect but not erase these differences. The morphological differences are not as striking as those separating the whole complex from other species, notably *P. taeda* and *P. echinata* (Smouse & Saylor, 1972), but they are adequate to prevent serious ambiguity everywhere but in the vicinity of the transition zone. In addition, there is some evidence of partial reproductive isolation between the two taxa (Smouse, 1970).

The most meaningful classification in the authors viewpoint is to follow Clausen (1939) in denoting these two taxa as subspecies: *Pinus rigida* Mill. subsp. *rigida*, and *P. rigida* subsp. *serotina* (Michx.) Clausen.

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STUDIES OF THE *PINUS RIGIDA-SEROTINA* COMPLEX II. NATURAL HYBRIDIZATION AMONG THE *PINUS RIGIDA-SEROTINA* COMPLEX, *P. TAEDA* AND *P. ECHINATA*[1]

PETER E. SMOUSE[2] AND LEROY C. SAYLOR[3]

ABSTRACT

Patterns of hybridization were studied among *Pinus taeda*, *P. echinata* and the *P. rigida-serotina* complex. Efforts were made to determine the relationships of these taxa to help clarify the taxonomic status of members of the *P. rigida-serotina* complex.

Hybridization between *Pinus taeda* and the *P. rigida-serotina* complex was common, and genetic exchange occurred in both directions. Hybridization between *P. echinata* and the *P. rigida-serotina* complex was more restricted, as was hybridization between *P. taeda* and *P. echinata*. All three of these entities (*P. taeda*, *P. echinata*, and the *P. rigida-serotina* complex) were found to maintain their separate integrities in sympatric populations, in spite of the hybridization.

The aforementioned species distinctions were contrasted with the cohesiveness of the types within the *Pinus rigida-serotina* complex, to explain further the decision by Smouse and Saylor (1973) to denote the components of the complex as subspecies: *P. rigida* subsp. *rigida* and *P. rigida* subsp. *serotina*.

The subsection *Australes* Loud. of the genus *Pinus* L. consists of a geographically cohesive assemblage of species which inhabit the eastern United States and the Caribbean. Individual species extend into Canada (*P. rigida* Mill.) and into Central America (*P. caribaea* Morelet). The geographic ranges of various species within this group overlap considerably, and it is common to find two or more species in intimate contact. Natural hybridization is not uncommon in sympatric populations, and genetic exchange is sometimes extensive enough to create taxonomic problems.

Natural hybridization between the *Pinus rigida-serotina* complex and *P. taeda* is one example. Hybridization between *P. taeda* L. and *P. rigida* Mill. subsp. *rigida* has been reported by Little *et al.* (1967), while similar hybridization between *P. taeda* and *P. rigida* subsp. *serotina* (Michx.) Clausen has been reported by Kang (1966)[4]. Preliminary field observations for the present study indicated the existence of considerable hybridization between *P. taeda* and the transitional type of the *P. rigida-serotina* complex. In addition, hybridization between *P. echinata* Mill. and *P. rigida* subsp. *rigida* has been reported (Austin, 1928).

Because of these complex hybridization patterns and because of previous

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[1] Paper number 3679 of the Journal Series of the North Carolina State University Agricultural Experiment Station, Raleigh, North Carolina, U.S.A. This study was supported, in part, by McIntire-Stennis funds (Project 4016) and by the National Aeronautics and Space Administration and the National Science Foundation, which provided fellowship support for the senior author.

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[4] The classification used in this paper for members of the *P. rigida-serotina* complex follows that proposed by Smouse and Saylor (1973).

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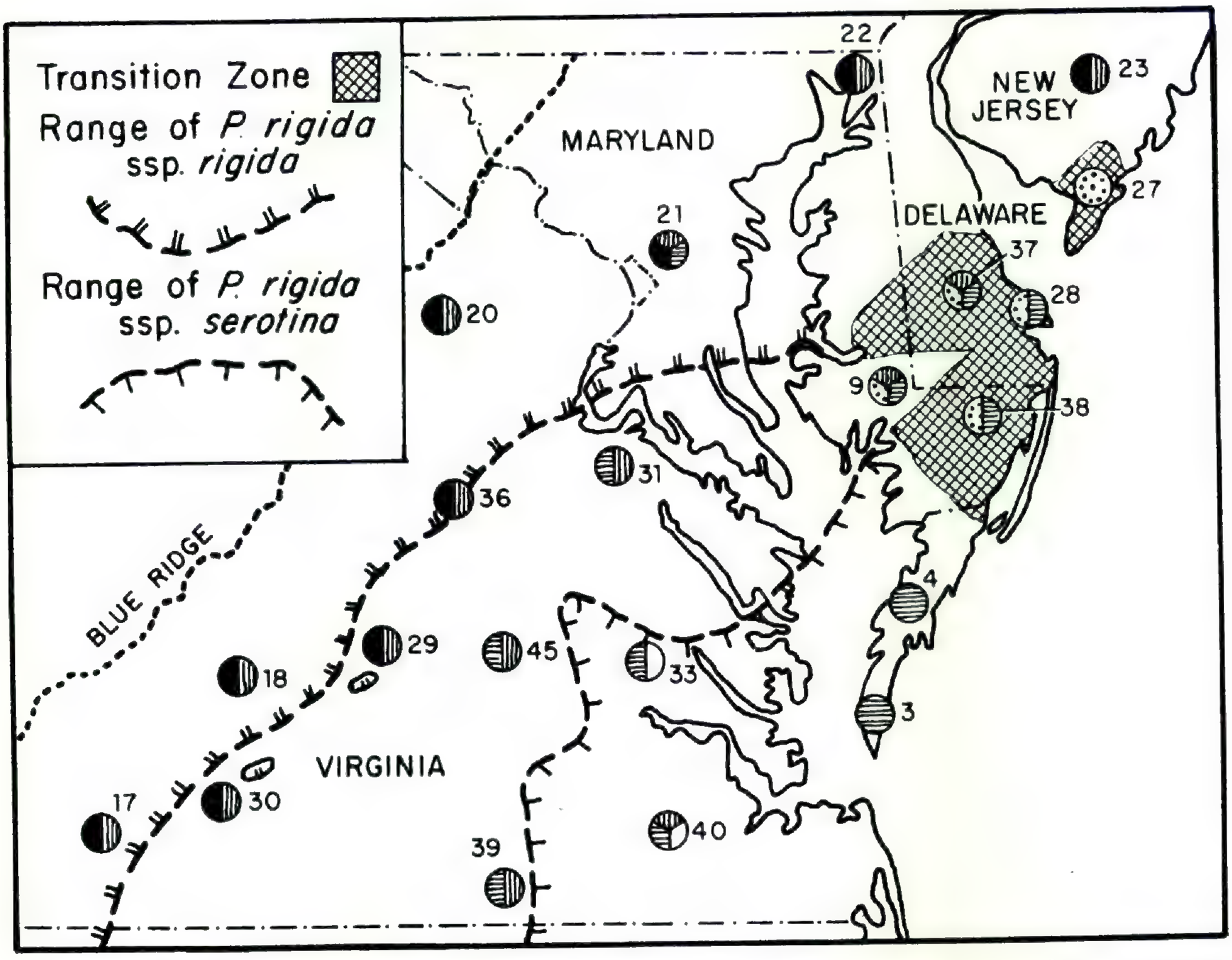

FIGURE 1. Population map of the study area, showing sample locations and taxa present. Solid shading, *Pinus rigida* subsp. *rigida*; no shading, *P. rigida* subsp. *serotina*; dotted shading, transitional type; horizontal shading, *P. taeda*; vertical shading, *P. echinata*.

taxonomic problems associated with members of the *P. rigida-serotina* complex, the present study was proposed to better determine existing relationships among all of these taxa. The specific objective of this paper is to describe the patterns of natural hybridization among the *P. rigida-serotina* complex, *P. taeda*, and *P. echinata* in and near the area of maximum sympatry of all three taxa.

SAMPLING AND MEASUREMENT PROCEDURES

A number of populations located within and near the geographic ranges of *Pinus rigida* subsp. *rigida* and *P. rigida* subsp. *serotina* and within the transition zone between them were chosen for sampling (Fig. 1). The geographic ranges of both subspecies, as well as those of *P. taeda* and *P. echinata*, extend considerably beyond the region sampled; this area was chosen because it represented the zone of maximum sympatry of all three components of the *P. rigida-serotina* complex with both *P. taeda* and *P. echinata*.

An attempt was made to obtain a representative sample of the trees growing at each location. Within each population, a square grid was superimposed upon the ground, utilizing a random starting point; distance between parallel lines of the grid was 50 feet. The nearest cone bearing tree to each grid intersection was selected for sampling. The number of trees sampled was determined by the following schedule:

1 species present	15 trees
2 species present	30 trees
2 species and hybrid suspects present	45 trees
3 species present	45 trees
3 species and hybrid suspects present	60 trees

The location and probable taxonomic identity of each tree sampled was recorded on a map. Populations with two or three species were seldom balanced as to representation in the sample, so an adjustment was necessary to insure an adequate sample of the rarer taxon or taxa. The trees of the most numerous taxon were assigned numbers which were drawn out at random without replacement until only 15 trees remained. The trees whose number had been drawn were deleted from the sample, and areas at the grid intersections represented by the deleted trees were resampled. The nearest tree not of the species deleted was then addd to the sample.

In addition to natural hybrids, it was possible to obtain samples from artificial F_1 hybrids of the following crosses: *Pinus rigida* subsp. *rigida* × *P. taeda* (located at the Wicomico State Forest, Maryland), and *P. rigida* subsp. *serotina* × *P. taeda* (located at the Westvaco Experimental Forest, Georgetown, South Carolina).

Seven morphological characters were utilized in this study. These traits were: needle length, fascicle sheath diameter, peduncle length, cone length, closed cone diameter, seed wing length, and seed thickness. The traits were chosen on the basis of: (1) accuracy of measurement, (2) availability from the largest number of trees sampled, (3) utility in separating the taxa under consideration, and (4) intermediacy of the values in F_1 hybrids.

Analysis and Results

The analysis proceeded in two stages. The first step was to adjust each taxon to the location in question by removing morphological variation associated with environmental differences. The second step was to determine which of the possible taxa constituted the most likely parents of each putative hybrid specimen and to determine the pattern of hybridization. These two operations are described in sections on *Geographic Variation* and *Canonical Analysis*.

Geographic Variation: Each of the four taxa exhibited morphological variation from population to population. Since it was desirable to analyze hybridization at each location separately, it was necessary to construct taxonomic standards of comparison which allowed for such geographic variation. While it was clear that each of the taxa actually growing at the location should be represented, it was also clear that a taxon need not be currently present to have been involved in hybridization.

For locations in and near the range of *Pinus rigida* subsp. *rigida*, putative hybrids were compared with *P. rigida* subsp. *rigida*, *P. taeda*, and *P. echinata*; whereas for those locations in and near the range of *P. rigida* subsp. *serotina*, putative hybrids were compared with *P. rigida* subsp. *serotina*, *P. taeda*, and *P. echinata*. For locations within the *P. rigida-serotina* transition zone, putative hybrids were compared with the transitional type, *P. taeda*, and *P. echinata*. The

threeway division of the locations into those with *P. rigida* subsp. *rigida*, those with *P. rigida* subsp. *serotina*, and those with the transitional type was based on the finding that the three taxa constituted a single geographically variable complex, in which only one type occurred at any given location (Smouse & Saylor, 1973).

Each taxonomic standard (an array of seven character means and a covariance matrix describing the variation) was constructed in one of two manners. If a taxon were actually present at the location, the character means for that population were used. The measure of variation employed was the average within population covariance matrix for that taxon.

If a taxon were not present, it was necessary to construct an abstract image of what it would look like if it had been present. Before this could be done, however, it was necessary to describe the association of the seven morphological variables with the geographic and environmental variation within each taxon. To accomplish this, information was used from a companion study (Smouse & Saylor, 1973) for *Pinus rigida* subsp. *rigida* and *P. rigida* subsp. *serotina* from populations to the north and south of the transition zone. The only samples of *P. taeda* and *P. echinata* available were those shown in Figure 1. The description of the association between morphological appearance and geographic location was accomplished by means of unweighted multiple regression analyses of the seven character variables on four environmental measures—(1) latitude, (2) elevation, (3) a measure of potential annual incident solar radiation, and (4) a measure of site productivity. The first two were used in logarithmic form, because a better description of geographic patterns was possible using the two variables in this form. The second two variables are defined in Smouse (1970) as are the computational details of the regression analyses.

The final result of this operation was a set of regression equations describing the association of morphological and environmental factors within each taxon. With this set of equations, it was possible to predict by standard multivariate regression procedures the seven character means and the corresponding covariance matrix for each of the taxa at any given location. (The estimated means and variances for all locations are given in Table 1.)

Canonical Analysis: Once the taxonomic standards for the three taxa were constructed at each location, it was possible to determine which taxa were the most likely ancestors of a particular hybrid specimen. The method employed was a canonical rotation of axes, details of which are described by Smouse (1972). This technique gives rise to a two dimensional, equilateral triangle of three species, which in turn can be divided into three hybrid regions (corresponding to three types of two-taxon hybrids) by bisecting the angles of the triangle (Figs. 2–4).

For the present study, the coordinates of each putative hybrid specimen at each location were plotted, along with those of artificial F_1 hybrids of *Pinus rigida* subsp. *rigida* × *P. taeda* and *P. rigida* subsp. *serotina* × *P. taeda* (Figs. 2–4). Preliminary laboratory designations were attached to each putative hybrid on the basis of a thorough visual examination.

It can be seen from the figures that the *a priori* and *a posteriori* designations

TABLE 1. Estimated population means and variances for the various taxa.

Population	Taxon[a]	Character means and variances[b]						
		Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
(03)	T	193(351)	213(443)	1(5)	86(105)	34(10)	24(11)	243(431)
	S+	176(527)	247(507)	11(11)	61(53)	41(21)	22(9)	164(221)
	E+	91(187)	162(307)	5(3)	47(30)	21(5)	18(4)	191(265)
(04)	T	177(351)	197(443)	0(5)	87(105)	33(10)	26(11)	255(431)
	S+	178(562)	252(541)	11(12)	63(56)	41(23)	21(10)	162(236)
	E+	92(192)	165(315)	6(3)	51(31)	23(5)	18(4)	187(272)
(33)	T	195(351)	247(443)	1(5)	82(105)	31(10)	24(11)	248(431)
	S	167(404)	248(445)	10(10)	60(46)	37(16)	22(9)	158(190)
	E+	86(175)	157(288)	6(3)	47(29)	21(4)	17(4)	187(248)
(39)	T	180(351)	231(443)	1(5)	81(105)	32(10)	24(11)	251(431)
	S+	185(583)	256(560)	13(13)	54(58)	35(23)	22(10)	167(244)
	E	82(117)	142(262)	6(2)	44(25)	20(4)	16(3)	189(244)
(40)	T	189(351)	233(443)	1(5)	84(105)	35(10)	27(11)	255(431)
	S	183(404)	256(445)	14(10)	58(46)	40(16)	22(9)	171(190)
	E	87(117)	156(262)	6(2)	44(25)	19(4)	16(3)	181(244)
(09)	T	189(351)	224(443)	1(5)	87(105)	36(10)	29(11)	254(431)
	RS	156(271)	259(273)	13(6)	64(33)	36(12)	25(5)	155(214)
	E	83(117)	157(262)	4(2)	45(25)	22(4)	17(3)	192(244)
(27)	T+	181(412)	232(583)	3(5)	85(117)	35(13)	27(13)	234(493)
	RS	129(271)	230(273)	5(6)	66(33)	40(12)	24(5)	165(214)
	E+	80(177)	163(290)	5(3)	44(29)	21(4)	16(4)	183(251)
(28)	T	187(391)	218(443)	4(5)	92(105)	38(10)	26(11)	224(431)
	RS	133(271)	250(273)	9(6)	67(33)	39(12)	23(5)	177(214)
	E+	84(190)	167(312)	4(3)	42(31)	20(5)	17(4)	190(270)
(37)	T	185(351)	227(443)	1(5)	88(105)	37(10)	26(11)	232(431)
	RS	151(271)	239(273)	8(6)	61(33)	38(12)	22(5)	170(214)
	E	78(117)	170(262)	7(2)	50(25)	22(4)	15(3)	180(244)
(38)	T	172(351)	231(443)	1(5)	78(105)	32(10)	24(11)	224(431)
	RS	148(271)	237(273)	8(6)	56(33)	34(12)	21(5)	153(214)
	E+	80(172)	157(282)	5(3)	44(28)	20(4)	16(3)	186(243)
(17)	T+	181(528)	231(748)	4(7)	71(150)	32(17)	23(17)	222(632)
	R	124(188)	255(403)	6(5)	55(44)	35(10)	20(7)	180(198)
	E	73(117)	145(262)	5(2)	42(25)	19(4)	15(3)	198(244)
(18)	T+	182(516)	266(732)	2(7)	83(147)	34(17)	25(17)	250(619)
	R	113(188)	230(403)	8(5)	56(44)	34(10)	22(7)	173(198)
	E	70(117)	139(262)	7(2)	44(25)	19(4)	15(3)	181(244)
(20)	T+	160(449)	217(567)	5(6)	69(134)	32(13)	25(14)	217(552)
	R	132(188)	243(403)	7(5)	56(44)	36(10)	21(7)	188(198)
	E	70(117)	145(262)	5(2)	41(25)	19(4)	14(3)	182(244)
(21)	T	171(351)	227(443)	3(5)	77(105)	32(10)	25(11)	233(431)
	R	129(188)	239(403)	8(5)	57(44)	35(10)	22(7)	176(198)
	E	75(117)	160(262)	5(2)	42(25)	20(4)	16(3)	182(244)

[a] R = *P. rigida* subsp. *rigida*
S = *P. rigida* subsp. *serotina*
RS = *P. rigida-serotina* transitional type
T = *P. taeda*
E = *P. echinata*
\+ = estimated by regression

[b] The characters are:
Y_1 = needle length (mm)
Y_2 = needle fascicle diameter (.01 mm)
Y_3 = peduncle length (mm)
Y_4 = cone length (mm)
Y_5 = cone diameter (mm)
Y_6 = seed wing length (mm)
Y_7 = seed thickness (.01 mm)
A(B): A = mean; B = variance.

TABLE 1. (continued)

Population	Taxon[a]	Character means and variances[b]						
		Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
(22)	T+	174(453)	246(642)	4(6)	80(129)	35(14)	26(15)	222(543)
	R	116(188)	236(403)	7(5)	56(44)	33(10)	21(7)	162(198)
	E	72(117)	154(262)	4(2)	40(25)	19(4)	14(3)	183(244)
(23)	T+	172(412)	225(583)	4(5)	78(117)	35(13)	26(13)	218(493)
	R	103(188)	216(403)	3(5)	58(44)	35(10)	22(7)	158(198)
	E	71(117)	158(262)	5(2)	44(25)	20(4)	16(3)	181(244)
(20)	T+	179(400)	246(567)	3(5)	78(114)	33(13)	25(13)	238(480)
	R	105(188)	247(403)	9(5)	69(44)	41(10)	25(7)	193(198)
	E	76(173)	145(285)	6(3)	43(28)	19(4)	16(4)	186(246)
(30)	T+	181(550)	260(780)	0(7)	86(156)	33(18)	26(18)	269(659)
	R	134(188)	239(403)	9(5)	62(44)	39(10)	23(7)	178(198)
	E	86(117)	158(262)	6(2)	47(25)	22(4)	17(3)	186(244)
(31)	T	169(351)	213(443)	3(5)	76(105)	33(10)	26(11)	238(431)
	R+	131(291)	240(463)	8(7)	59(50)	37(12)	22(8)	175(218)
	E	88(117)	152(262)	7(2)	46(25)	20(4)	16(3)	183(244)
(36)	T+	172(389)	236(552)	3(5)	77(110)	33(12)	25(13)	238(466)
	R	135(188)	249(403)	10(5)	55(44)	35(10)	21(7)	173(198)
	E	79(117)	147(262)	7(2)	45(25)	20(4)	16(3)	180(244)
(45)	T	157(351)	220(443)	2(5)	85(105)	34(10)	26(11)	255(431)
	R+	150(317)	241(504)	10(8)	60(55)	38(13)	23(8)	184(238)
	E	71(117)	139(262)	6(2)	51(25)	21(4)	16(3)	182(244)

are generally compatible. Almost all of the specimens which are "misclassified" fall within the confidence limits of one or the other of the parental taxa; these had been designated in the laboratory as likely advanced generation segregants. It would be difficult in most such cases to be sure of the donor parent, but the laboratory designations were felt to be reliable.

It is possible to construct a central region for specimens derived from genetic exchange involving all three taxa, but the fact that known F_1 hybrids between pairs of taxa sometimes occupied a rather central position suggested that the technique was not sensitive enough to detect such specimens with any precision. In addition, there was no visual evidence of complex hybridization in these populations, and the possibility was therefore ignored.

It is readily apparent from Figures 2–4 that there is no difficulty in distinguishing among *Pinus taeda*, *P. echinata*, and the *P. rigida-serotina* complex in sympatric populations. The morphological variations encountered within each of these taxa, as indicated by the confidence elipses of the three figures, show no overlap, and separation is complete. The various taxa therefore are separately recognizable entities in sympatric populations, in spite of natural hybridization.

In the case where the covariance matrices of the three taxa are identical, the three sides of the triangle correspond exactly to the two-taxon discriminant functions often employed in hybridization analysis. In that case, two-taxon hybridization patterns can be described by simply projecting the hybrids perpendicularly onto the appropriate side of the triangle. As pointed out by Smouse (1972), the position along the line can be used as an estimate of the relative proportions of ancestry contributed by the two parental taxa. For example,

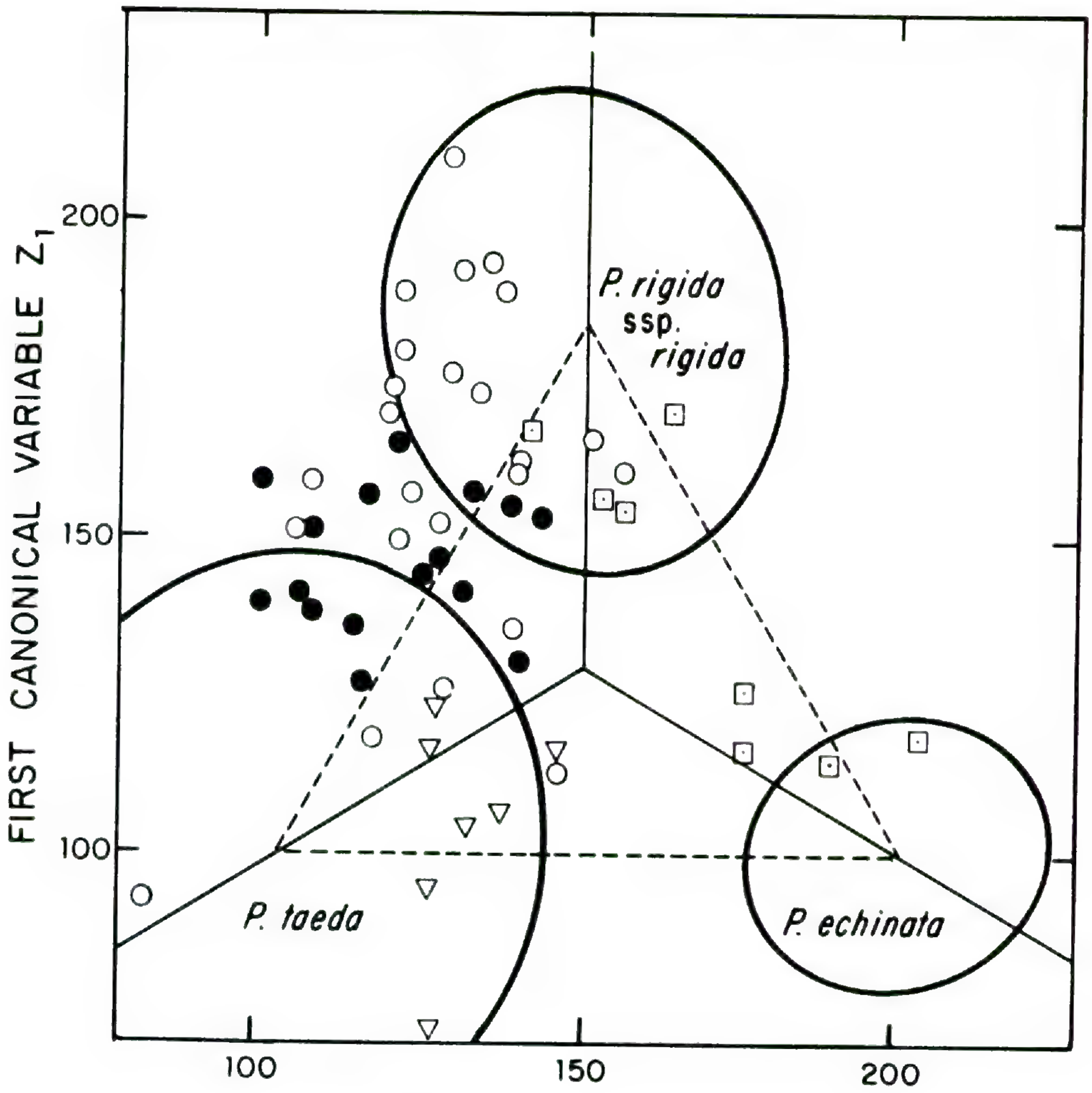

FIGURE 2. Canonical analysis of populations in and near the range of *Pinus rigida* subsp. *rigida*. Solid circles, experimental F_1 hybrid of *P. rigida* subsp. *rigida* × *P. taeda*; open circles, putative natural hybrid of *P. rigida* subsp. *rigida* × *P. taeda*; squares, putative natural hybrid of *P. rigida* subsp. *rigida* × *P. echinata*; inverted triangles, putative natural hybrid of *P. taeda* × *P. echinata*; large elipses denote 95% confidence contours.

backcross derivatives are closer to the recurrent parent. Although the covariance matrices of the various taxa are not completely identical, separate two-species analyses were made, and these showed patterns of hybridization very similar to those illustrated in Figures 2–4.

The artificial *Pinus rigida* subsp. *rigida* × *P. taeda* F_1 hybrids occupy the center of the corresponding side of the triangle, as expected. Genetic exchange, as indicated by the direction of backcrossing, occurs in both directions (Fig. 2). Separate analysis of individual locations showed that backcrossing was primarily in the direction of the more abundant parental taxon for a given location. A similar situation exists for *P. rigida* subsp. *serotina* and *P. taeda* (Fig. 3). Although genetic exchange between *P. taeda* and the *P. rigida-serotina* transitional type occurred in both directions, the transitional type served as the primary recipient of genetic material.

Hybridization between *Pinus echinata* and *P. taeda* resulted in backcrossing

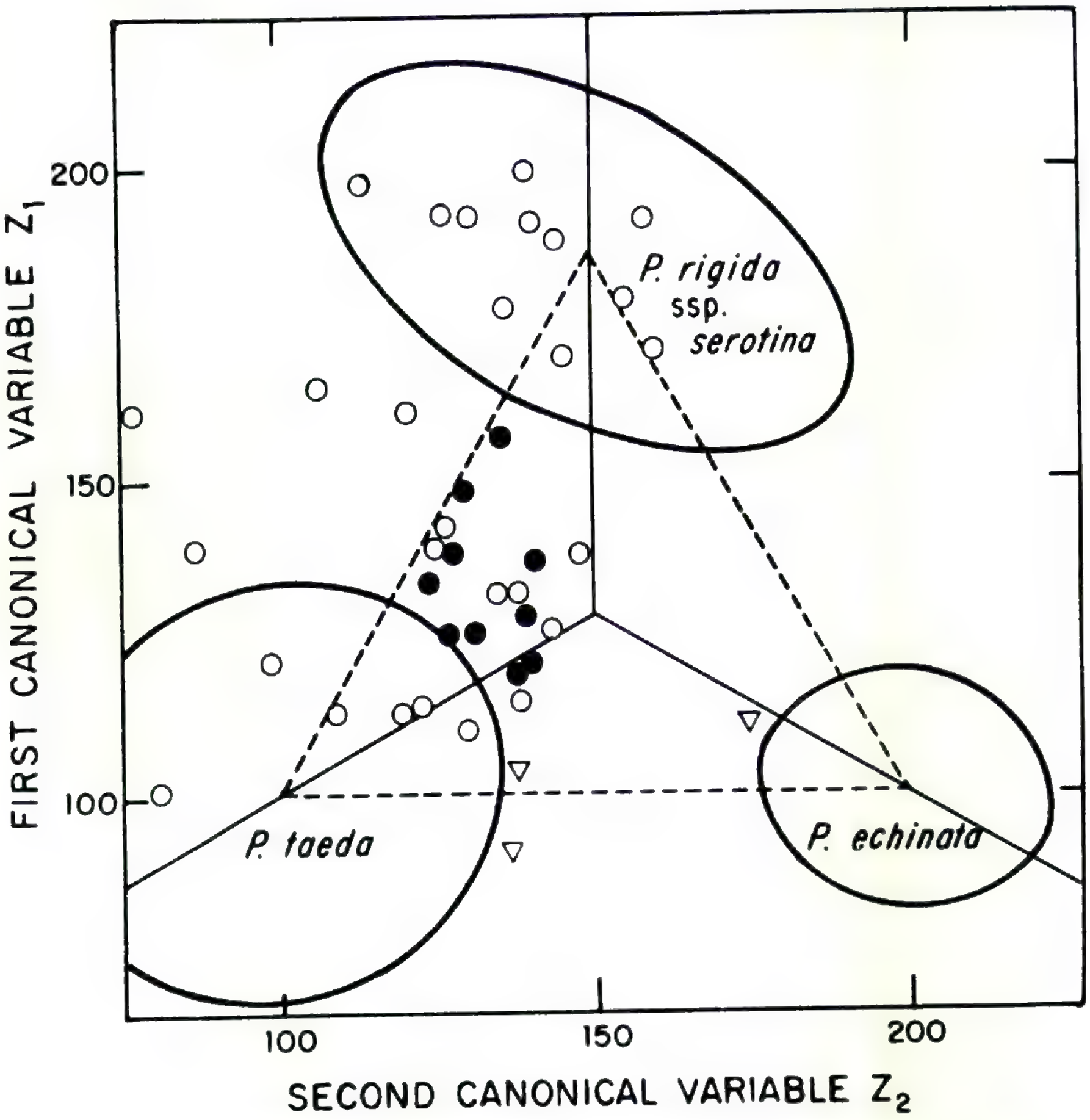

FIGURE 3. Canonical analysis of populations in and near the range of *Pinus rigida* subsp. *serotina*. Solid circles, experimental F_1 hybrid of *P. rigida* subsp. *serotina* × *P. taeda*; open circles, putative natural hybrid of *P. rigida* subsp. *serotina* × *P. taeda*; inverted triangles, putative natural hybrid of *P. taeda* × *P. echinata*; large elipses denote 95% confidence contours.

primarily in the direction of *P. taeda* (Figs. 2–4), while genetic exchange between *P. echinata* and *P. rigida* subsp. *rigida* occurred in both directions (Fig. 2). Hybridization between *P. echinata* and the transitional type was too rare to adequately categorize (Fig. 4), and no hybridization was detected between *P. echinata* and *P. rigida* subsp. *serotina* (Fig. 3). It should be pointed out that sympatric occurrence of *P. echinata* with both of the latter was rather limited.

DISCUSSION AND CONCLUSIONS

Whether or not the "advanced generation segregants" were possibly species representatives was a matter of some concern in this study. If their classifications were altered arbitrarily, it is possible that the patterns of hybridization illustrated in Figures 2–4 would change. To check this possibility, all putative hybrid specimens within each of the confidence contours were reclassified as species representatives, and the analyses were repeated. The results were negligibly different for the putative hybrid specimens not inside the confidence contours.

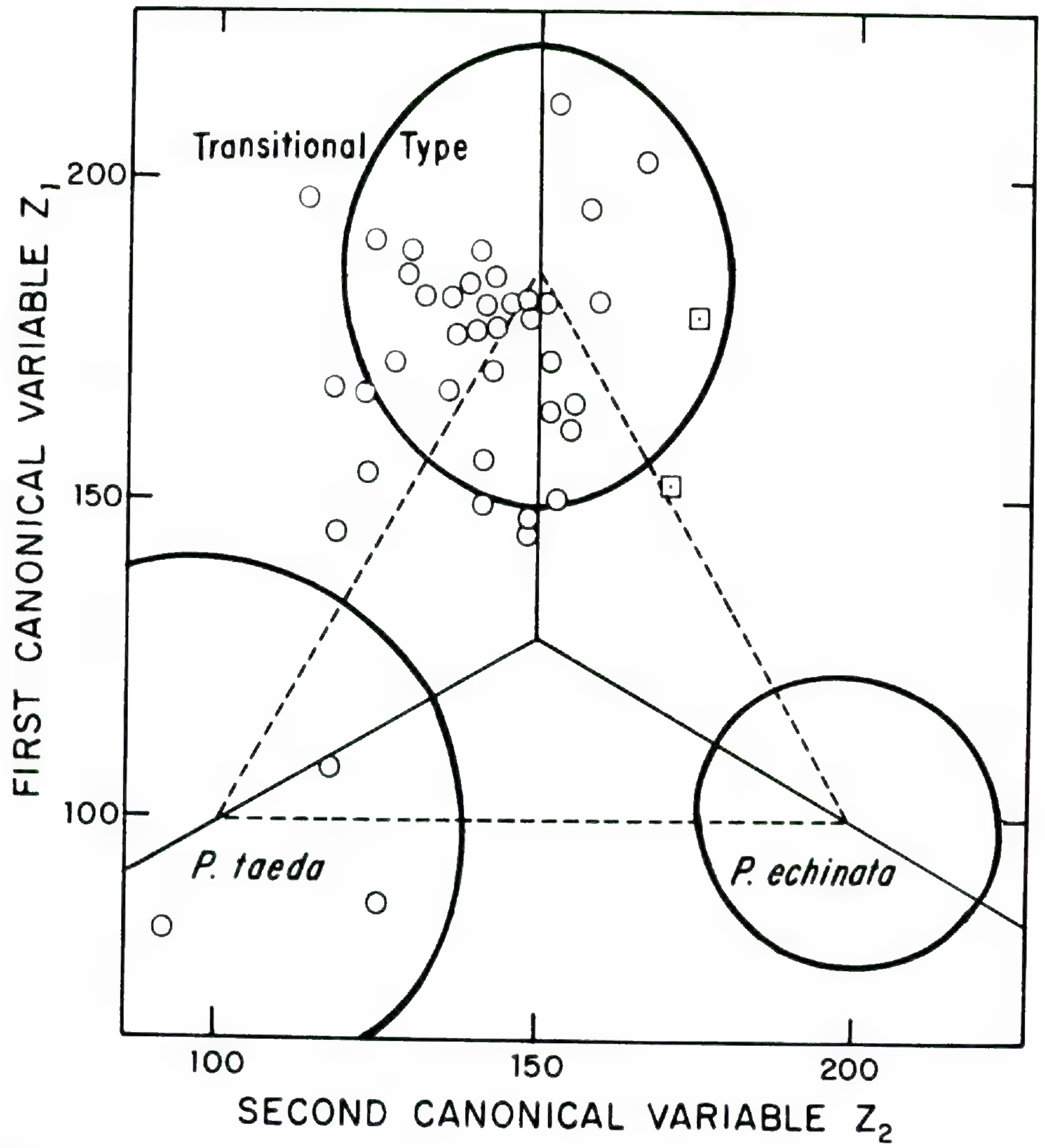

FIGURE 4. Canonical analysis of populations in and near transitional zone. Open circles, putative natural hybrid of transitional type × *Pinus taeda*; squares, putative natural hybrid of transitional type × *P. echinata*; large elipses denote 95% confidence contours.

It is of interest to compare the pattern of hybridization encountered between *Pinus rigida* subsp. *serotina* and *P. taeda* in the present study with that found by Kang (1966), who found no evidence for backcrossing with the former. Most of the populations in that study were very much dominated by *P. taeda*, whereas a range of species frequencies was sampled in the present study. It may be that the difference in the results of the two studies reflect this difference in the types of populations sampled. It would seem reasonable that populations dominated by *P. taeda* would show a preponderance of *P. taeda*-like hybrid derivatives.

Interpretation of the hybridization between the transitional type and *Pinus taeda* rests very heavily on the treatment of the transitional type as a clinal intermediate between the two subspecies of *P. rigida* (Smouse & Saylor, 1973). In view of the amount of hybridization occurring between *P. taeda* and the transitional type, however, the question might well be raised as to whether the structure of the transitional type can be adequately resolved without reference to

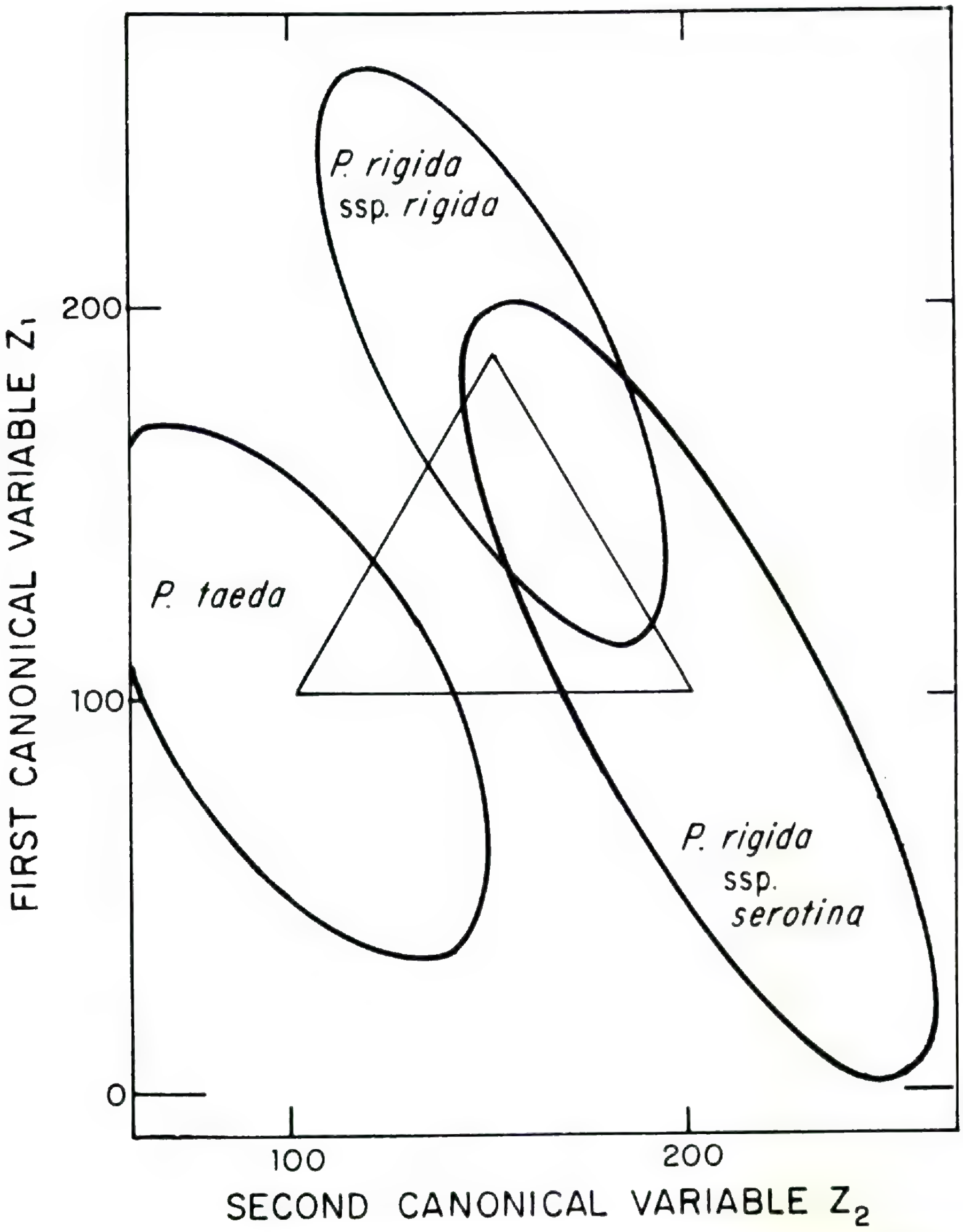

FIGURE 5. Canonical triangle of *Pinus rigida* subsp. *rigida*, *P. rigida* subsp. *serotina*, and *P. taeda*. Large elipses denote 95% confidence contours.

P. taeda. The relationships among the three taxa and the transitional type can be portrayed by recourse to the canonical technique employed earlier; in this case the taxa were placed at the corners of the triangle, and 95% confidence contours were computed for each (Fig. 5).

The attenuated shape of the confidence elipses resulted from the considerable stretching of scales necessary to separate the subspecies of *Pinus rigida*. The overlap between them was still considerable, as was expected on the basis of similar results reported by Smouse and Saylor (1973). The transitional type was intermediate between the subspecies of *P. rigida*, and it showed a slight tendency

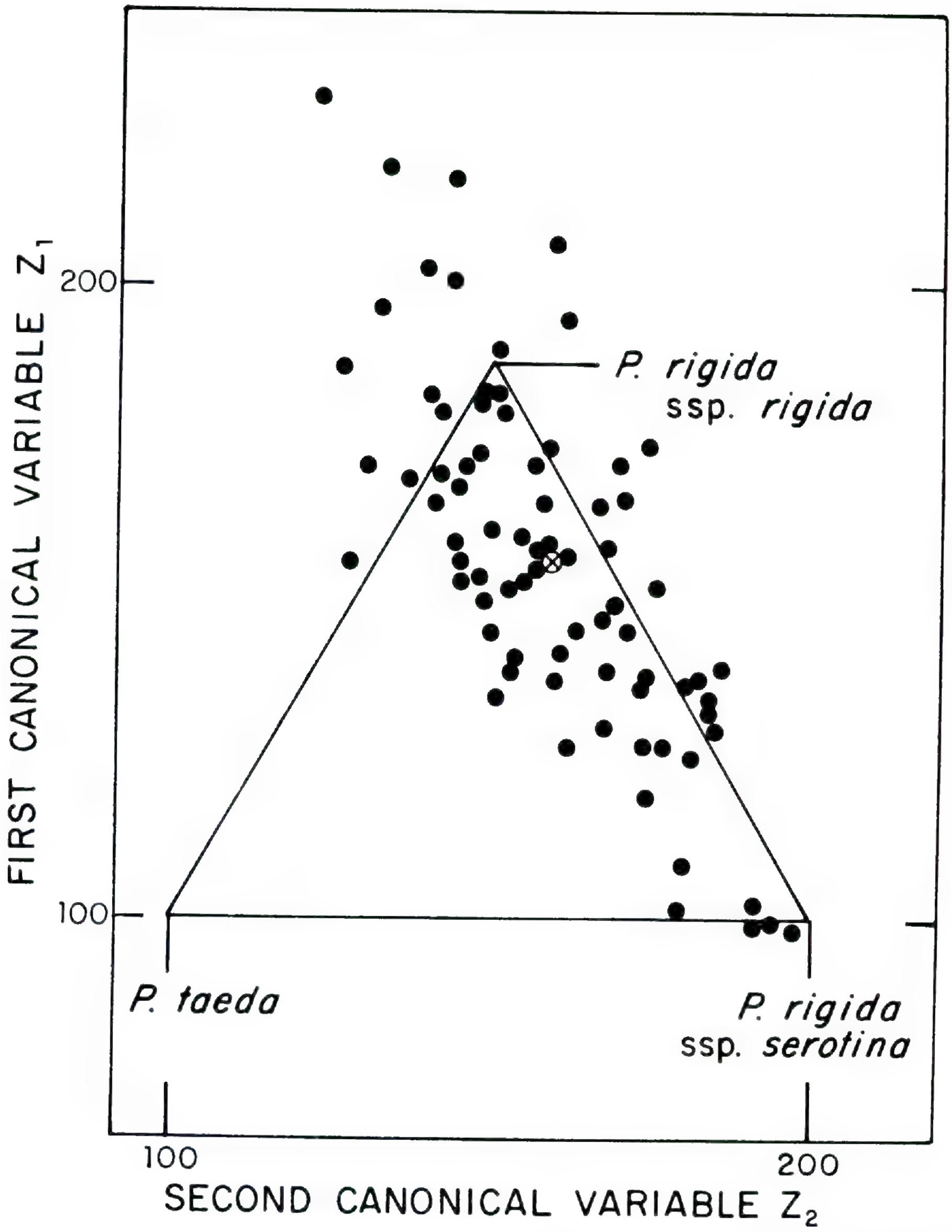

FIGURE 6. Canonical analysis of transitional type. Solid circles, transitional specimens; *X*-ed circle, average of the transitional type.

to cluster on the *P. taeda* side of the *P. rigida-serotina* axis (Fig. 6). This tendency was only slightly exaggerated by adding the *P. taeda* × transitional type hybrids to the transitional type, which should be evident from Figure 4. It therefore appears that there has been a pervasive, but minor contribution of *P. taeda* to the gene pool of the transitional type.

Based on the results of this and other related studies, several conclusions were considered valid regarding crossing patterns and taxonomic status. Hybridization between *Pinus taeda* and the *P. rigida-serotina* complex has been common, and genetic exchange, as indicated by the pattern of backcrossing, occurs in

both directions. Primary genetic infiltration, however, is into the *P. rigida-serotina* complex. *Pinus echinata* was found to hybridize with *P. taeda*, *P. rigida* subsp. *rigida*, and the *P. rigida-serotina* transitional type, but this hybridization is more limited than that involving *P. taeda*. Both *P. taeda* and *P. echinata* are clearly distinct from the *P. rigida-serotina* complex in sympatric populations, in spite of the hybridization. Because these three taxa maintain their separate integrities, it was felt that this was corroborative evidence for considering the complex as a species (equal in distinction to *P. taeda* and *P. echinata*) which is composed of two subspecies, *P. rigida* subsp. *rigida* and *P. rigida* subsp. *serotina*.

The distinctness of *P. taeda*, *P. echinata*, and the *P. rigida-serotina* complex stands in marked contrast to the lack of distinctness within the complex itself. The morphological cohesiveness and clinal continuity of the subspecies of *P. rigida* are even more striking when their separation from other taxa is considered.

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CONTRIBUTIONS TO THE KNOWLEDGE OF *MORAEA* (IRIDACEAE) IN THE SUMMER RAINFALL REGION OF SOUTH AFRICA[1]

PETER GOLDBLATT[2]

ABSTRACT

This paper comprises a preliminary revision of *Moraea* in the summer rainfall area of South Africa. A brief review of taxonomic history and a summary of morphological characters of the genus is followed by the taxonomic treatment. *Moraea* is divided into five groups or series not equivalent to formal taxonomic ranks. Twenty-seven species and eight subspecies are recognised. Eleven new species and eight subspecies are described.

The genus *Moraea*, a geophytic, herbaceous perennial, is scattered throughout sub-Saharan Africa. Like most genera of the family in Africa, it occurs mainly in mountain regions, except in the south, where it achieves maximum development and is found in all situations. Although the majority of species occurs in the winter rainfall region of the Cape Province and the widest range of forms is found here, the genus is very well represented in the summer rainfall area, a fact not generally known because of our poor knowledge of the genus in this region.

The need for a workable and natural taxonomy of the genus in the summer rainfall region is twofold, for not only is there no general treatment at present, but also, because certain species are highly poisonous to sheep and cattle, there is a more immediate reason for a revision. As soon as a correct taxonomy for the group can be produced, it will be easier to study the species from this important practical aspect, as pointed out by N. E. Brown (1929).

Because of limitations in time, and the inadequacies of our knowledge of the genus in many parts of South Africa, the present paper has many deficiencies, and no claim is made for this this work to be a definitive study. It is quite clear that many aspects of the genus, particularly the *Moraea spathulata* complex, require further study in the field. It is hoped rather that this work will provide a basis for further investigation and will serve to indicate those aspects least understood.

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[1] I am grateful to those in charge of the herbaria at the following institutions for making available their material for study: Albany Museum, Grahamstown; Bolus Herbarium, Cape Town; Natal Herbarium, Durban; Botany Department, Rhodes University, Grahamstown; Botanisches Museum, Berlin-Dahlem; British Museum (Natural History), London; Cathedral Peak Forest Station; Compton Herbarium, Cape Town; Government Herbarium, Stellenbosch; Royal Botanic Gardens, Kew; Muséum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris; National Herbarium, Pretoria; Naturhistoriska Riksmuseet, Stockholm; the herbarium at the University of Lesotho, Swaziland and Botswana at Roma.

I also wish to thank Professor E. A. Schelpe for making available facilities at the Bolus Herbarium where the study was undertaken; to Mrs. Margo Branch who provided the illustrations; to Dr. F. Ferrario of the Geography Department of the University of Cape Town for aid with the Latin descriptions; to my wife for drawing the maps and for her help in preparing the manuscript. Finally, my appreciation is extended to the C.S.I.R. of South Africa for grants which made possible the many collecting trips during the course of the study.

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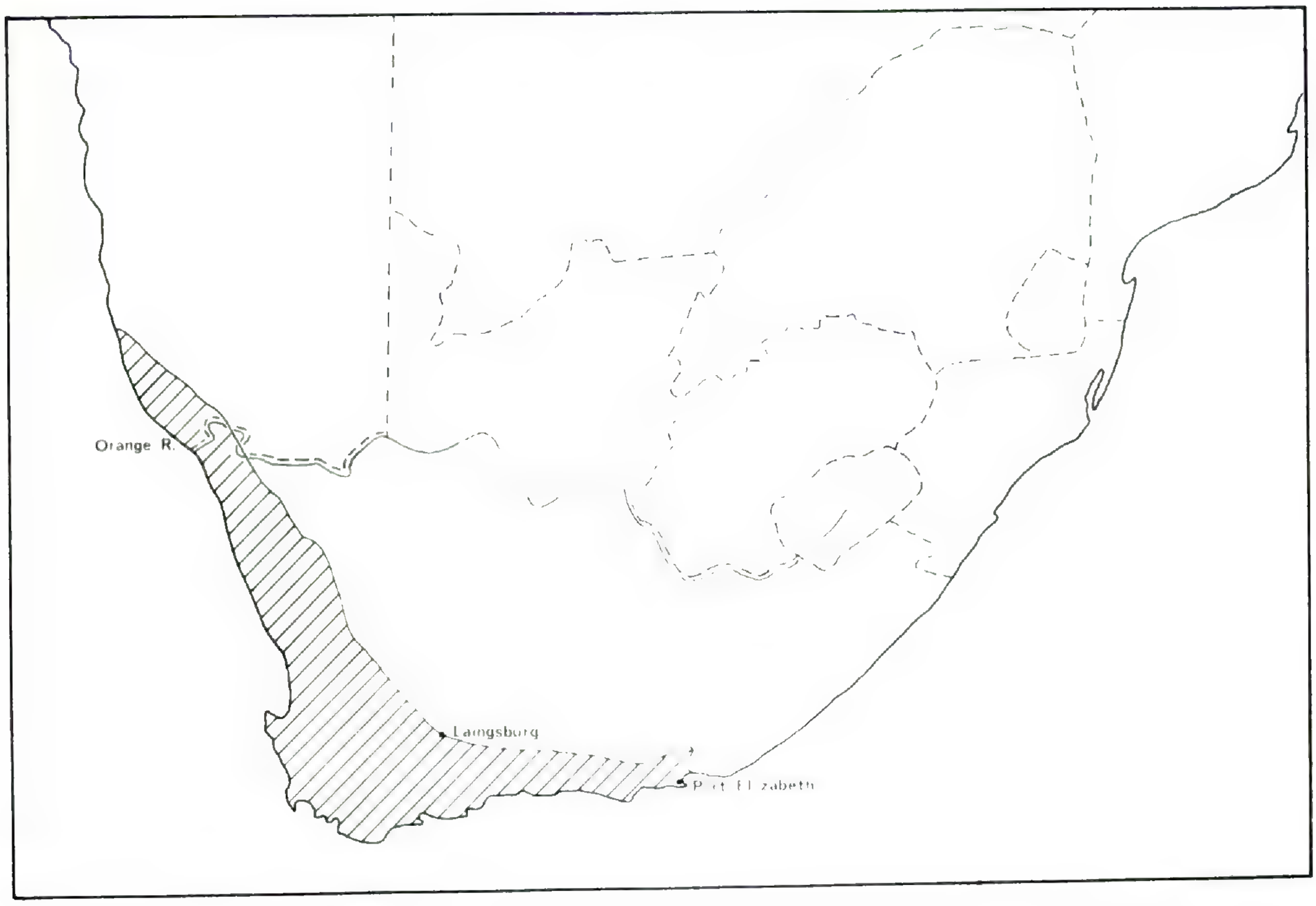

FIGURE 1. Map of South Africa showing the winter rainfall region (shaded).

DEFINITION OF THE SUMMER RAINFALL AREA AS DEALT WITH HERE

In the present treatment, 26 species and one subspecies of a species typical of the winter rainfall area are recognised as summer rainfall representatives, but several more occur within this zone, although these are predominantly winter rainfall species. To accurately define the limits of the summer rainfall region is not possible, for there is considerable overlap of summer and winter rainfall cycles in the eastern Cape and in the karoo, and of course, areas of the southern Cape may receive rain all year round. In these areas, several members of the genus typical of one or other rainfall type occur together, each responding to the appropriate season. Somewhat arbitrarily, a dividing line has been drawn from Port Elizabeth in the south, through Laingsburg, and then northwards to the Orange River. The region to the west of this line is not dealt with here except in the case of *Moraea spathulata* which, though a typical member of the summer rainfall group, occurs as far west as the George district. This division (Fig. 1) is approximately equivalent to the line between areas receiving either more than 60% of their rain in summer or less than 60% of their rain in summer (Adamson, 1938).

A key has been designed to allow identification of all the species recorded or known to occur in what is regarded as summer rainfall area, but *Moraea ciliata*, *M. polyanthos*, and *M. viscaria*, which are clearly typical winter rainfall area elements, are not dealt with further.

OUTLINE OF TAXONOMIC HISTORY

The most complete general treatment of *Moraea* is found in *Flora Capensis* (Baker, 1896), the standard reference which is now quite out of date. In this work Baker recognised 45 species of *Moraea*. Two of his subgenera, *Dietes* and *Helixyra* (now *Gynandriris*), are at present regarded as separate genera, leaving 37 species of *Moraea*, of which only 8 are regarded as occurring in the summer rainfall area. Subsequent to *Flora Capensis* several species from the summer rainfall area were described, the most significant contribution being that of N. E. Brown (1929) who, although he dealt only with the Transvaal, recognised 17 species, 13 of these being new to science.

Brown's work is now also out of date, not only because he ignored species outside the Transvaal, but he tended to recognise far too many species, several of which, it is now clear, were identical. His work was, however, valuable in drawing attention to the genus in the Transvaal. No doubt the paucity of material available at that time and lack of knowledge of the living plants were a distinct handicap, and when this is appreciated, his work must be admired.

The way in which Brown dealt with species in his article on Transvaal Iridaceae would today be regarded as somewhat cavalier. The formal descriptions, even of new species, are poor or sometimes absent although types are clearly indicated, and it is only through the medium of the rather detailed key that species can be identified. This key must be regarded as embodying part, if not the entire description of some species. In spite of this treatment, all his species of *Moraea* have been identified quite readily and are all recognised as validly described, even though many have been reduced to synonymy here.

Subsequent to N. E. Brown's work, little attention was paid to the summer rainfall Moraeas until quite recently when J. Robert Sealy of the Royal Botanic Gardens, Kew, and then Mrs. A. A. Mauve of the Botanical Research Institute, Pretoria, began, through the medium of *Curis' Botanical Magazine* and *Flowering Plants of Africa* respectively, to revive interest (Sealy, 1965; Obermeyer, 1970*a*, *b*). Mrs. Mauve rediscovered and redescribed some of N. E. Brown's species as well as one quite new plant. Her studies and collections of *Moraea* over the years have helped considerably in elucidating the taxonomy of the genus, and the present author is much in her debt.

A NOTE ON SPECIES CONCEPTS

There is considerable difficulty in distinguishing and defining species of *Moraea* from the often poorly prepared herbarium specimens. All too frequently these are incomplete, usually with corms and prophylls lacking, or else flowers are crumpled and discoloured; thus it is inevitable that some specimens are misidentified. One particular characteristic, *i. e.* whether plants are solitary or grow in clumps, is regarded as extremely significant, but unfortunately this is often impossible to determine from herbarium material. Sometimes this is the only usable key character, as in distinguishing some forms of *M. moggii* and *M. spathulata*. If this is not obvious from the specimen, or if field notes are absent, determination is difficult.

In deciding whether a race merited taxonomic recognition, not only morpho-

logical characters were weighed, but factors such as distribution, flowering time, growth form, and habitat were considered. The value of these criteria assumes great importance in some groups. In the groups *Caeruleiflora* (comprising small, usually blue-flowered species) and *Grandiflora* (tall, usually yellow-flowered species), flower morphology is often similar in related races or at least indistinguishable in dried specimens, so that vegetative characters and whatever other information can be obtained, must be considered. In contrast, in the group *Vieusseuxia*, flower morphology, especially the nature of the inner perianth segments is so distinctive as to leave little doubt about species limits and therefore ecological data are not so important in classification. This is not to suggest that species are any less "good" in some sections, and in fact when working primarily from dried material, it is difficult to determine whether or not too broad a view of the group is being taken, leading to the recognition of too few or too many species. In such cases the practical aspects of taxonomy are a consideration in deciding the rank of a race or taxon which, although recognisable, has no good diagnostic feature.

Description and Morphology of the Genus

Moraea is treated by most authors as a member of the tribe (or subfamily) Irideae and as a close ally of the Northern Hemisphere genus *Iris*. There is little doubt that *Iris*, *Dietes*, and *Gynandriris* are all closely related to *Moraea*, and care must be taken to ensure that plants believed to be *Moraea* are not confused with these genera. *Moraea* can be distinguished from *Iris* and *Dietes* by the nature of the rootstock, which is invariably a corm in *Moraea*, whereas *Iris* and *Dietes* have a rhizome or bulb; and from *Gynandriris* in which there is a sterile prolongation of the ovary forming a pseudo-perianth tube. The often-mentioned difference between *Iris* and *Moraea*, the presence or absence of a perianth tube, is not an invariable distinction, for *M. cooperi* has a well developed perianth tube, while in some species of *Iris* this character may be poorly developed.

THE CORM

The corm is derived from a lateral bud formed on the lowermost or lower nodes of the scape and is one internode long with a bud at its apex. The adventitious roots arise just below the bud, *i. e.* near the apex of the corm. It is covered by a tunic, *i. e.* a special leaf covering the corm alone, and often by other materials derived from the decaying remains of previous seasons' leaf bases, prophylls, and corm tunics.

THE FOLIAR APPENDAGES

There are three different types of leaf structures produced in *Moraea*, the prophylls, *i. e.* brown, dry, sheathing basal leaves, a produced green leaf or leaves, and short bract-like leaves which are entirely sheathing and have no free apex.

Prophylls: Up to four in number, these sheath the underground part of the scape and seldom extend much above ground level. They are membranous to rigid, pale to dark brown and may be entire, irregularly broken, or fibrous, all these features being of considerable taxonomic value (Fig. 2).

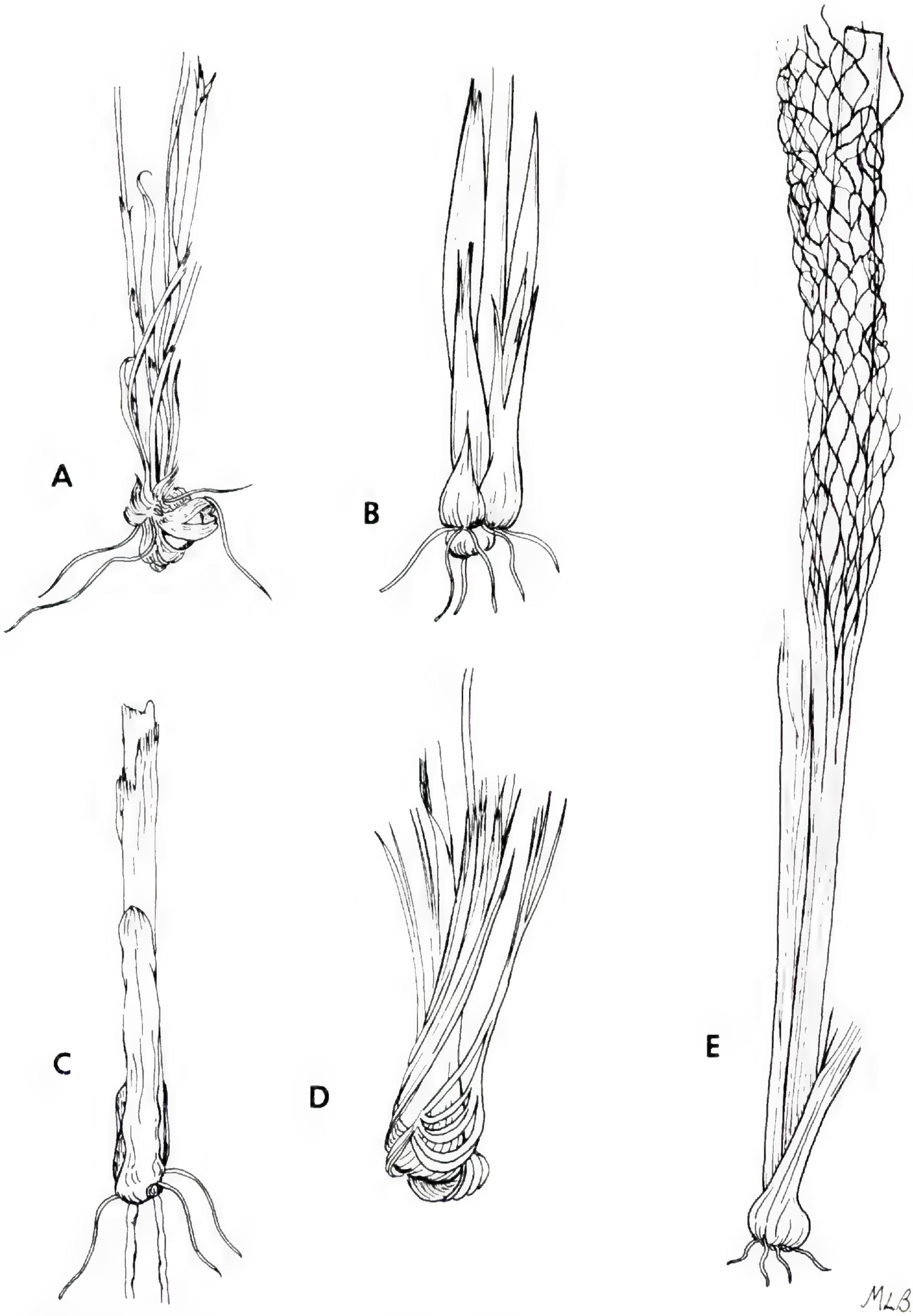

FIGURE 2. Prophylls of the *Grandiflora* group of *Moraea*.—A. *M. muddii*.—B. *M. spathulata* subsp. *transvaalensis*.—C. *M. graminicola*.—D. *M. galpinii*.—E. *M. alticola*. [A and D × ⅔; B, C and E × ⅓.]

Produced leaves: The major assimilatory organs are the long, well developed leaves inserted on the stem at any point from ground level to the base of the inflorescence. The base of the leaf completely sheaths the scape, but distally it is free, usually linear and dorsiventral with a short equitant apex. The leaf number is usually constant in a species, and the number can range between one and six. The majority of summer rainfall Moraeas have only a single leaf.

Bract leaves: These foliar organs are reduced leaves which sheath the scape. Produced at nodes, they sometimes subtend branches, but the latter are often absent. The bract leaves completely sheath the scape above the node with only the acute apex free. Although usually green and herbaceous, the bract leaves often have a dry scarious apex. Where the aerial part of the scape is poorly developed, there is little distinction between the bract leaf and true leaf, as in *Moraea ciliata.*

THE SCAPE

The aerial part of the stem is termed the scape here and is considered the peduncle of the inflorescence. The degree of branching is very variable in the genus, and the nature and number of branches were the main criteria used by Baker (1892) in dividing the genus into sections. This character is used to some extent in the present paper, as in distinguishing the group *Acaules* where the scape does not grow above ground.

THE INFLORESCENCE

The inflorescence in *Moraea* is cymose in development. There is a variable number of flowers per inflorescence, ranging from up to 20 in *M. ciliata* to only one in *M. cooperi.* The inflorescence is enclosed in two opposed bracts termed spathes here, and these generally resemble the bract leaves closely. In addition to the spathes, the individual flowers are also subtended by smaller transparent membranous bracts which are seldom visible, being enclosed in the larger spathes. The flowers are borne one by one and are extruded from the spathes on a slender pedicel. The fruit develops either outside the inflorescence spathes as in most species, or within the spathes as in members of section *Acaules* where the pedicel contracts after flowering has occurred.

THE FLOWERS

Perianth. The flower of *Moraea* is, although variable, the feature which defines the genus (Fig. 3). The flowers are actinomorphic, lack a perianth tube, except in *M. cooperi* (a winter rainfall species), and have unguiculate petals or perianth segments. The outer three are usually larger, the claw slender and bearded, and the limb reflexed and hanging downward. At the base of the limb there is usually a prominent "eye" or nectar guide. The inner petals are more variable. They are typically held erect, though the limb may be held outwards or be reflexed like the outer petals as in *M. inclinata* and *M. polystachya.* In other species the inner petals are reduced so that there is no expanded limb, or the apex may be three-lobed or three-pronged (species in the group *Vieusseuxia*) (Fig. 3).

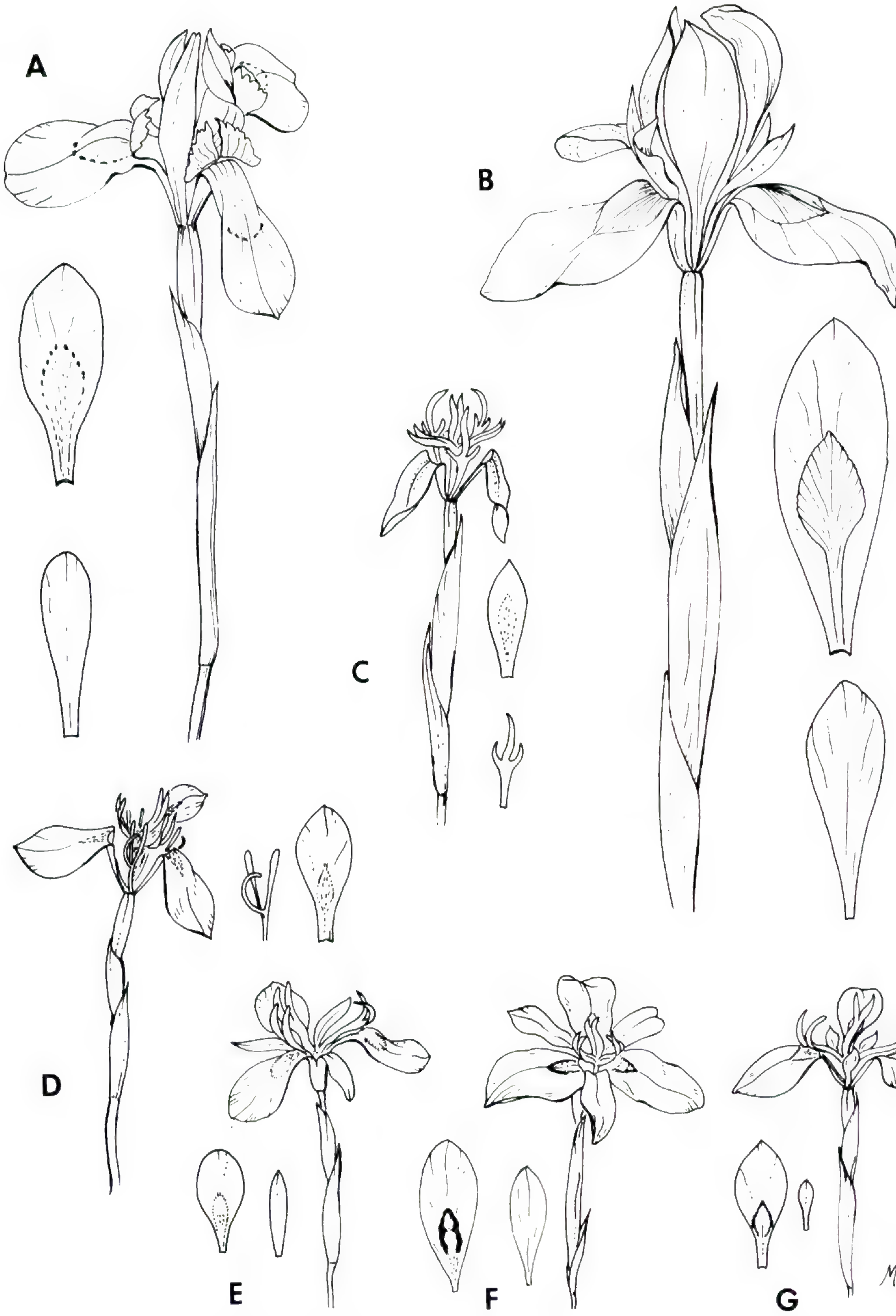

FIGURE 3. Flowers and perianth segments of summer rainfall species of *Moraea*.—A. *M. huttonii*.—B. *M. spathulata* subsp. *spathulata* (both group *Grandiflora*).—C. *M. trifida*.—D. *M. pubiflora* subsp. *brevistyla* (both group *Vieusseuxia*).—E. *M. elliotii*.—F. *M. inclinata*.—G. *M. algoensis* (last three all group *Caeruleiflora*). [All flowers about × ⅔.]

Stamens. The three stamens are similar in all species with the filaments, inserted opposite the outer perianth segments, being either free but contiguous in the lower part, or more often fused in the lower half. The anthers lie closely pressed against the style branches extending up to the stigma lobe, though in some species they exceed the stigma (*e. g. Moraea trifida*).

Gynoecium. The tricarpellate, inferior ovary is linear to clavate in shape, usually round in section, but triangular in some species. The style is short, dividing below the base of the anthers into three large, flat, petaloid style branches. The branches diverge, each lying fairly close or appressed to the claw of the outer petal. Near the apex of each style branch on the abaxial side are the stigmatic lobes, and above these the style branch forks to form two crests, which are usually long and well developed.

THE FRUITS AND SEEDS

The fruit is a loculicidal capsule which exhibits considerable variation in size and shape. Its taxonomic use is limited, because it is seldom collected and is even unknown in some species. The seeds are either small and angular and without an inflated testa (groups *Visciramosa*, *Caeruleiflora*, and *Vieusseuxia*), irregular in shape, with a soft spongy testa (group *Acaules*), or large, depressed and somewhat triangular or flattened, often with a somewhat spongy testa (group *Grandiflora*).

Subgeneric Classification

In his treatment of the genus in *Flora Capensis*, Baker divided *Moraea* into several subgenera and sections. As already mentioned, two of his subgenera, *Gynandriris* (as *Helixyra*) and *Dietes*, are now regarded is distinct genera, leaving *Moraea* and *Vieusseuxia*. These last mentioned were distinguished by the nature of the inner perianth segment, this in *Moraea* being a large, entire structure, while in *Vieusseuxia* it is small and often tricuspidate. This distinction does not hold for all species, and *Vieusseuxia* is not regarded as a distinct subgenus here. It is proposed instead that it be treated as a group of equal rank with several other groups of the genus. It is beyond the scope of this paper to revise the sections of the genus as established by Baker, because this would require detailed study of the winter rainfall species. Instead, all formal subgeneric ranks are ignored, and related species are treated together in groups. As the present paper deals with only 27 species in detail, there should be no difficulty in disregarding the formal ranks between genus and species. The groups are arranged as follows:

Group I: **Acaules**

This group corresponds to Baker's section *Acaules*. It comprises three species, only one of which occurs in regions receiving summer rainfall alone. The characteristic features are lack of aerial stem, similarity of leaves and spathes, and a contractile pedicel.

Group II: **Visciramosa**

Although predominantly a winter rainfall area group, one of the three to four species in the group, *Moraea viscaria*, occurs as far west as Grahamstown and must therefore be mentioned. The characteristics of the group are the sticky internodes and well developed branching the whole length of the scape.

Group III: **Caeruleiflora**

This group does not correspond exactly to any of Baker's sections, but includes species which he placed in both *Corymbosae* and *Subracemosae*. The group *Caeruleiflora* comprises species with small to medium sized blue flowers. Branching may be extensive or considerably reduced (Fig. 3E–G).

Group IV: **Vieusseuxia**

Baker's subgenus *Vieusseuxia* is treated as a group here, although its circumscription is somewhat altered. *Vieusseuxia* is closely allied to the group *Caeruleiflora* and a dividing line is difficult to draw. *Vieusseuxia* is characterised by reduced branching and modified inner perianth segments, which may be cusp-like, trifid, or absent (fig. 3C–D).

Group V: **Grandiflora**

This group comprises part only of Baker's *Monocephalae*. As shown by Goldblatt (1971) the *Monocephalae* are an artificial group, with the Cape elements *Moraea angusta* and allies not closely related, although they are morphologically similar. These Cape species are not regarded as belonging to the group *Grandiflora*, which as treated here occurs solely in the summer rainfall region with one species, *M. spathulata*, extending as far west as George in the southern Cape. The group is characterised by large, usually yellow flowers, very limited or no branching and depressed to disciform seeds (fig. 3A–B).

NOTE ON CITATION OF SPECIMENS

The arrangement of specimens examined, following the taxonomic treatment and discussion of each species, is based on the system currently gaining acceptance in South Africa (Edwards & Leistner, 1971). The system is based on a grid, and geographical degrees of latitude and longitude define each grid which is numbered accordingly. The one degree square grids are also designated by the name of a major town within it. Grids are divided into four quarters labelled from left to right A, B, C, or D and these quarter degree squares are again divided into four and labelled A, B, C, or D. Thus, all specimens are cited with data localising them to one-sixteenth of a degree square.

In one detail the method used here diverges from the usual in that countries and provinces are not stated. This is because many species occur along the borders of the provinces and of the small countries of Lesotho and Swaziland, so that: a) is often impossible to know in which area certain collections were made (this is especially true in the Drakensberg where many species occur along the border which Lesotho shares with Natal and the Cape); b) the citing of many grids in two areas would have been unnecessarily repetitive.

The herbarium of the Cathedral Peak Forest Station has been abbreviated as CPF and the herbarium at the University of Lesotho Swaziland and Botswana at Maseru as ROML.

Key to the Groups[3]

1. Produced leaves not distinct from bract leaves or inflorescence spathes; stem not or barely produced above ground, enclosed by leaves or bracts ..... Group II: Acaules
1′. Produced leaves distinct from bract leaves and inflorescence spathes; stem produced above the ground.
2. Plants much branched, branches parallel to stem for short distance, then bending at right angles; sticky below nodes ..... Group I: Visciramosa
2′. Plants unbranched or not branching as above; not sticky below nodes.
3. Inner perianth segments with an expanded limb, at least 1.5 mm wide, entire and not three-lobed or tricuspidate.
4. Produced leaves one only; outer perianth segments more than 3.5 cm long; if less, then yellow flowered ..... Group V: Grandiflora
4′. Either produced leaves more than 2 or if one only, then outer perianth segments less than 3.3 cm long and flowers blue ..... Group III: Caeruleiflora
3′. Inner perianth segments three-lobed to tricuspidate, or linear, without expanded limb, and less than 1.5 mm wide ..... Group IV: Vieusseuxia

Keys to the Species

Group I: Visciramosa

One species only, in the summer rainfall area, *Moraea viscaria*. It grows primairly in the winter rainfall region.

Group II: Acaules

1. Leaves glabrous: corm tunics of dark or black, fine, closely woven fibres ..... 1. *M. falcifolia*
1′. Leaves ciliate to pubescent; corm tunics of pale, coarse fibres ..... *M. ciliata*[4]

Group III: Caeruleiflora

1. Produced leaves more than one.
2. Outer perianth segments usually more than 3.3 cm long; flowering December to July ..... 2. *M. polystachya*
2′. Outer perianth segments usually less than 3.0 cm long; flowering August to October ..... *M. polyanthos*[4]
1′. Produced leaf solitary.
3. At time of flowering, leaf dead, or if newly emergent, then not attached to the flowering stalk.
4. Plants small, rarely to 10 cm high; inflorescence spathes less than 3 cm long; flowering in summer on Drakensberg summit plateau ..... 7. *M. alpina*
4′. Plants usually more than 12 cm high; inflorescence spathes more than 3 cm long; flowering in winter and spring, rarely in November, in grassland ..... 6. *M. stricta*
3′. Leaf present and well developed at time of flowering and attached to flowering stalk at ground level or above.
5. Leaf inserted on scape just below inflorescence (at least two-thirds of scape below leaf insertion).
6. Capsule spherical; outer spathe bracts deep brown, and less than half the length of inner spathe ..... 5. *M. inclinata*
6′. Capsule ovoid to clavate; outer spathe bracts green rarely uniformly brown and at least half the length of the spathe.

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[3] With regard to dimensions of floral characters it must be stressed that wherever possible measurements were made from live material or carefully laid out floral parts. Poorly dried flowers invariably appear smaller than in life and this must be borne in mind when using the key.

[4] Primarily a winter rainfall area species which is not dealt with in this paper.

7. Inflorescence more than 3.5 cm long; outer perianth segments more than 2 cm long ..... 3. *M. elliotii*
7′. Inflorescence usually less than 3.5 cm long (rarely to 4 cm); outer perianth segments rarely to 2 cm long ..... 4. *M. natalensis*

5′. Leaf inserted near ground level, rarely higher up (but usually at least one-half of scape above the leaf).
8. Inner perianth segments less than 1.2 cm long; limb comparatively broad ..... 8. *M. algoensis*
8′. Inner perianth segments more than 1.2 cm long; linear-lanceolate, with limb not distinctly enlarged above ..... 3. *M. elliotii*

Group IV: VIEUSSEUXIA

1. Inner perianth segments entire, not divided into distinct lobes.
2. Outer perianth segments more than 2.5 cm; flower white ..... 10. *M. albicuspa*
2′. Outer perianth segments less than 2.5 cm; flower white veined with mauve ..... 12. *M. modesta*

1′. Inner perianth segments divided into three distinct lobes or cusps.
3. Inner perianth segments comprising one long central cusp and two small lateral lobes.
4. Plant leafless when flowering, if leaf present then not attached to flowering stalk.
5. Inner perianth segments more than 1 cm long, reaching above stigmas ..... 14. *M. marionae*
5′. Inner perianth segments less than 1 cm long, not reaching stigmas ..... 12. *M. modesta*
4′. Basal green leaf present at flowering time and attached to flowering stalk.
6. Cusp of inner segment erect; outer segments seldom more than 6 mm wide ..... 13. *M. trifida*
6′. Cusp of inner segment incurved or spirally twisted; outer segments usually more than 10 mm wide ..... 15. *M. bellendenii*

3′. Inner perianth segments consisting of one long, slender, acute central cusp and two long, obtuse lateral cusps.
7. Inner perianth segment spotted or white ..... 9. *M. pubiflora*
7′. Inner segments uniform blue-purple ..... 11. *M. dracomontana*

Group V: GRANDIFLORA

1. Prophylls submembranous, white to pale, entire or frayed or torn at apex only.
2. Plants always solitary in low altitude grassveld; flowering in spring or summer, occurring in Natal and eastern Cape ..... 21. *M. graminicola*
2′. Plants solitary or in small clumps on rocky hilltops; flowering summer; occurring in the Transvaal ..... 25. *M. spathulata* subsp. *saxosa*

1′. Prophylls brown to black, entire or irregularly broken or fibrous.
3. Prophylls of flowering individual split regularly into rigid, dark brown-black, vertical bristles, innermost prophyll not forming a network above ..... 22. *M. galpinii*
3′. Prophylls of flowering individual brown to black, brittle, entire or irregularly broken, but not forming rigid vertical bristles, or innermost sheath sometimes forming a brown to pale reticulum above (old, outer prophylls sometimes becoming fibrous).
4. Occurring along watercourses; rarely solitary; style crests marked with a dark contrasting blotch at base ..... 27. *M. huttonii*
4′. Not occurring along watercourses; solitary or in clumps; style crests not marked at base.
5. Flowers not predominantly yellow to white, but either pink, mauve, blue, or grey.
6. Filaments longer than anthers; flowers marked and flushed flesh pink to purple ..... 19. *M. carnea*
6′. Filaments shorter than anthers; flowers slate blue to mauve ..... 20. *M. ardesiaca*
5′. Flowers white to yellow.
7. Plants fairly small, seldom exceeding 40 cm; solitary; basal leaf slender, glaucous; usually less than 6 mm broad; outer perianth segments rarely more than 4.5 cm long.

8. Bract-leaves one only ..... 18. *M. unibracteata*
8′. Bract-leaves more than one ..... 17. *M. muddii*

7′. Plants large, seldom below 50 cm; solitary or in clumps; basal leaf rarely less than 5 mm wide; outer segments up to 8 cm long, rarely less than 4.5 cm.
9. Leaf terete (with narrow adaxial groove), margins inrolled; solitary in grassland in Natal midlands ..... 23. *M. hiemalis*
9′. Leaf flat to canaliculate, not terete; solitary or in clumps.
10. Prophyll produced upwards forming a well-developed, pale, fibrous network around lower part of leaf.
11. Leaf surface flat, margins usually thickened; plants growing in clumps ..... 26. *M. alticola*
11′. Leaf surface canaliculate, margins not thickened; plants usually solitary ..... 24. *M. reticulata*
10′. Prophyll not forming a network round base of leaf, or if network produced, then poorly developed and plants caespitose with canaliculate leaves.
12. Plants solitary with slender canaliculate leaf ..... 16. *M. moggii*
12′. Plants growing in clumps, rarely solitary; leaf flat to canaliculate ..... 25. *M. spathulata*

Group I: Visciramosa

Only one species of this group occurs in the summer rainfall region, namely *Moraea viscaria* (Thunb.) Ker. It is primarily a winter rainfall region species but extends eastwards to the Port Elizabeth-Grahamstown area. As it is not a true member of the summer rainfall flora, it is not dealt with further.

Group II: Acaules

1. **Moraea falcifolia** Klatt, Erganz. 32. 1882. Type: "Hantam Geb.," *Meyer s. n.* (B, holotype; S, isotype).

Moraea fasciculata Klatt, Erganz. 32. 1882. Type: "Langevaley," *Drége 2600* (B, holotype; K, P, S, isotypes).
Moraea galaxioides Baker, Handbook Irid. 49. 1892. Type: Transvaal, *Barber s. n.* (K, holotype).

Plants small, to 5 cm high, forming a sessile rosette. *Corm* conical, covered by strong coarse dark reticulate fibres, often bearing numerous cormlets at the base. *Prophylls* membranous, transparent. *Leaves* several, some indistinguishable from inflorescence spathes, slender, canaliculate, to 10 cm long, loosely coiled or linear, margins frequently undulate. *Stem* not produced above ground, simple or branching at or below ground to give rise to one to several inflorescences. *Flowers* (poorly known) white to cream with yellow nectar guides, pedicel contractile, shrinking after flower dies; *outer perianth segments* 1.5–2.2 cm long, claw somewhat less than half the length, claw to 1.5 cm wide; *inner segments* 1.3–2 cm long. *Filaments* to 6 mm long, joined in the lower half, anthers 3–4 mm long, white. *Style* about 5 mm long, branches to 8 mm and crests to 6 mm long. *Ovary* clavate, capsule borne near ground level, soft walled, rotund, about 1 cm long. *Seeds* small and spherical or slightly angled.

Flowering time: May to November.

Distribution: Throughout the northwestern Cape, karoo, and in the northern Cape and western Transvaal (Fig. 4).

This species can easily be recognized by its dwarf, stemless habit. The

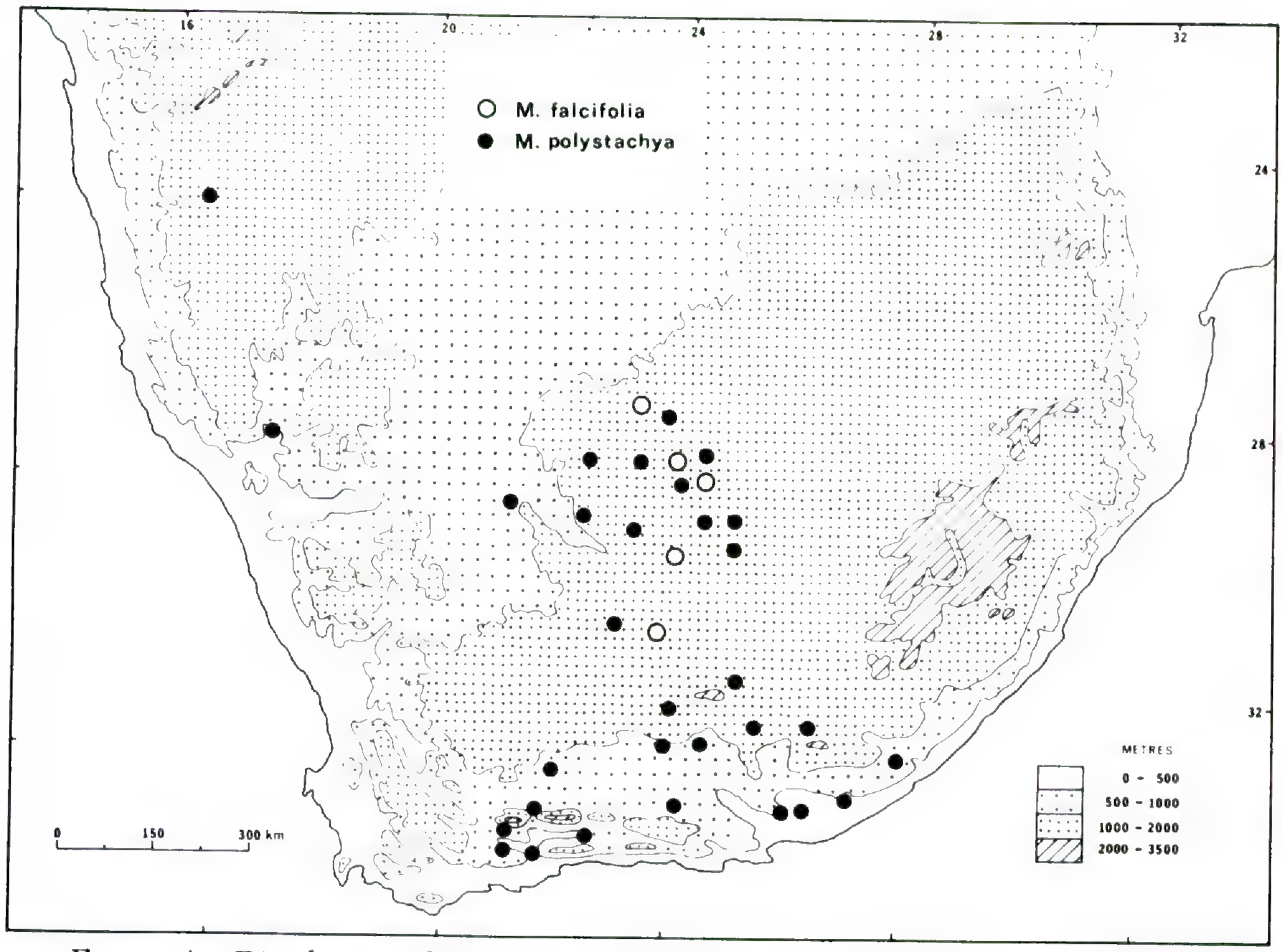

FIGURE 4. Distribution of *Moraea polystachya* and *M. falcifolia* (summer rainfall area only).

flowers are extremely fugaceous and are thus not well known although the plant has been collected frequently. The peculiar character of the contractile pedicel is also found in *Moraea cilata*, a related species occurring widely in the winter rainfall area and the margins of the summer rainfall area.

Moraea fasciculata is reduced to synonymy here. This species, the type of which was collected in the Langevlei area near Lambert's Bay on the west coast of the Cape Province, is a more slender form of *M. falcifolia*. This form does not appear to differ fundamentally from *M. falcifolia*, slender individuals of which may also be found in some populations.

Moraea galaxioides, also treated here as conspecific with *M. falcifolia*, appears to represent the extreme eastern form of the species. The type of *M. galaxioides* was collected in the western Transvaal and is a form with shorter, more rigid leaves. Specimens matching these occur at Kimberley, while further west in the Barkly West district, plants have larger leaves and can barely be distinguished from the winter rainfall area populations. A close examination of plants in the northeastern Cape reveals a cline in which leaves grade from the falcate or loosely coiled and undulate-margined type to a short, more rigid type towards the extreme eastern part of the range.

27.23 (Kuruman): Batlharos (-AD), *Silk 67* (BOL).
28.24 (Kimberley): Witfontein, Barkly West, *Acocks 2482* (BOL); Diamond Fields, *Tuck s. n.* (K); Klip Drift, Vaal River (-DA), *Barber s. n.* (K).
29.24 (Hopetown): Newlands, Barkly West (-AD), *Paton s. n.* (BOL 30838).
30.24 (De Aar): De Aar (-CA), *Wilman s. n.* (BOL 13940).

Group III: Caeruleiflora

2. **Moraea polystachya** (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805.

Iris polystachya Thunb., Diss. Iride no. 40. 1782. Type: *Thunberg* in Herb. Thunb. (UPS).
Moraea toxicaria Dinter, Feddes Repert. 19: 237. 1923, *nom. nud.*
Moraea venenata Dinter, Feddes Repert. 19: 238. 1924. Type: Bullsport, S.W.A., *Dinter 2141* (SAM, isotype).
Moraea polystachya var. *brevicaulis* Stent *ex* Phillips, Bot. Survey S. Africa Mem. 9: 16. 1926. Type: Stent & Curton, Bull. Dept. Agric. S. Africa 1922(6): *fig.* 2. 1922.

Plants medium to large, to 80 cm high. *Corm* to 5 cm in diameter, covered with hard, dark coarse fibres. *Prophylls* to 3, membranous, truncate. Leaves 3–5, linear, canaliculate, to 50 cm long and 0.6–2 cm wide. *Bract leaves* 6–12 cm long, dry in old plants. *Scape* erect, much branched. *Inflorescence* to 6 cm long, spathes green or turning brown, outer shorter than inner. *Flowers* blue with yellow to orange nectar guides; *outer perianth segments* to 5.5 cm long and to 2.5 cm wide; *inner segments* to 4.5 cm long and about 1.5 cm wide, reflexed. *Filaments* joined to apex, to 1 cm long; *anthers* about 1 cm long. *Style* 1 cm long, branches about 1 cm and crests to 2 cm long. *Ovary* clavate, surface wrinkled and red-veined; *capsule* ovoid, about 1 cm long; seeds, small, firm, angled. *Chromosome number* $2n = 12$, Riley (1962); *Goldblatt* 88 (J), 221 (BOL); *Tolken* 3985 (BOL).

Flowering time: Autumn and winter (December) March to July (August).

Distribution: Widespread in karoid regions, but occurring also in South West Africa, the eastern and northern Cape, western Orange Free State and western Transvaal (Fig. 4).

Icones: Batten & Bokelmann, Wild Flowers of the Eastern Cape Province, *Tab. 34, fig. 1.* 1966; Marloth, Flora of S. Africa 4: *Tab. 39A.* 1915; Obermeyer, Fl. Pl. Africa 35: *Tab. 1385.* 1962; Stent & Curton, Bull. Dept. Agric. S. Africa 1922(6): *fig.* 2. 1922.

Moraea polystachya is a common and widespread species. It has long been known to be poisonous to cattle. Some morphological variation occurs locally, and this is particularly noticeable in the number and width of the leaves; flower size is less variable. The variety *brevicaulis* figured by Stent (Bull. Dept. Agric. S. Africa 6) and described by Phillips, is not recognised here, as this dwarf form is known to occur occasionally as a seasonal variant in areas where plants are normally tall. It is not known whether the dwarf habit is always a seasonal response or whether some populations are invariably short.

The two species described by Dinter, *Moraea toxicaria* and *M. venenata*, from South West Africa, are treated as synonyms following Sölch (1969). Both fall within the range of form found in *M. polystachya*.

The closest ally of *Moraea polystachya* is *M. polyanthos* (Thunb.) Ker, which occurs in the Little Karoo and adjacent areas north of the Swartberg and flowers in the spring, usually during September and October. The distribution of the two species does overlap to a limited extent, but the flowering time, while not completely distinct, serves to isolate the species. *Moraea polyanthos* is a generally smaller plant with usually only three narrow leaves and smaller flowers than those of *M. polystachya*. A critical analysis of *M. polyanthos* is beyond the scope

of this paper, but it is clear that a detailed study of this species is required to determine its relationship with *M. polystachya.*

A second species, *Moraea carsonii* Baker, which occurs in central Africa, also bears a strong resemblance to *M. polystachya.* Though generally smaller in most characters, *M. carsonii* is remarkably similar to *M. polystachya.* This central African species awaits detailed study.

24.16 (South West Africa): Bullsport (-AB), *Strey 2061* (BOL), *Strey s. n.* (BOL 30835).
27.17 (South West Africa): Huns mountains (-CA), *Tolken 3985* (BOL).
28.21 (Upington): Between Upington and Keimos (-CA), *Glover s. n.* (BOL 13366).
28.22 (Glenlyon): Andriesfontein (-BA), *Rogers s. n.* (BOL 12588); Bingap (-CD), *Acocks 5770* (BOL).
28.23 (Griekwastad): Danielskuil (-BA), *Lawson s. n.* (BOL 30837).
28.24 (Kimberley): Windsorton (-BC), *Hall 649* (NBG); near Kimberley (-DB), *Potgieter 1470* (BOL), *Lewis 304* (SAM).
29.23 (Douglas): Mazelsfontein (-BA), *Anderson 545* (BOL).
29.24 (Hopetown): Modder River (-BB), *Harris s. n.* (BOL 30834).
29.25 (Jagersfontein): Petrusburg (-AB), *Potts 1370* (BOL); Fauresmith (-CB), *Henrici 2749* (BOL).
30.23 (Britstown): Giesenskraal (-CB), *Wilman s. n.* (BOL 30836).
31.23 (Victoria West): Near Murraysburg (-D), *Tyson 329* (BOL).
31.25 (Steynsburg): Grootfontein, Middelburg (-AC), *Gill 225* (BOL).
32.24 (Graaff Reinet): Near Aberdeen (-AC), *Taylor 464* (BOL); near Graaff Reinet (-BC), *H. Bolus 42* (BOL).
32.25 (Somerset East): Near Cradock (-BA), *F. Bolus s. n.* (BOL 30833).
32.26 (Fort Beaufort): Ventersdrift, Upper Kei, *Wells sub Galpin 6847* (BOL).
32.27 (Stutterheim): Kabousie River near Komgha (-DB), *Flanagan 1803* (BOL).
33.20 (Montagu): Wittepoort (-AD), *Esterhuysen 3503* (BOL); Riet Kloof, Laingsburg (-B), *Lewis 716* (SAM); between Ratelfontein and Montagu (-C), *Lewis 4428* (SAM); near Barrydale (-D), *Compton 19623* (NBG); near Lemoenshoek (-DD), *Leighton s. n.* (BOL 21735).
33.21 (Ladismith): Roodeberg summit (-DA), *Lewis 737* (SAM).
33.24 (Steytlerville): Near Steytlerville (-A), *Compton 19635* (NBG).
33.26 (Grahamstown): Alicedale (-AC) *Potts 983* (BOL); Grahamstown (-BC), *Rogers 27740* (BOL), *Schonland 1652* (SAM).
33.27 (Peddie): Peddie (-AA), *Barker 7822* (NBG).
Doubtful locality: Transvaal, *McLea s. n.* (BOL 5789).

3. **Moraea elliotii** Baker, Handbook Irid. 58. 1892. Type: Marshes near Lake Chrissie, *Scott-Elliot 1592* (K, holotype).—FIG. 3E.

Moraea macra Schl., Jour. Bot. 36:377. 1898. Type: Queenstown, *Galpin 2193* (B, holotype, BOL, PRE, isotypes).
Moraea stewartae N. E. Br., Trans. Roy. Soc. S. Africa 17: 346. 1929. Type: Hlatikulu, Swaziland, *Miss Stewart 44,* (K, holotype, PRE, isotype).
Moraea violacea Baker, Bull. Herb. Boiss., sér. 2. 1: 863. 1901. Type: Byrne, Natal, *Wood 5220* (Z, holotype, BM, isotype).
Moraea juncifolia N. E. Br., Trans. Roy. Soc. S. Africa 17: 346. 1929. Type: Saddleback, *Galpin 859* (K, holotype, SAM, isotype).

Plants medium in size, reaching to 55 cm in height. *Corm* to 2 cm in diameter, tunics of dark brown fairly coarse fibres often forming a neck extending upwards a short distance. *Prophylls* membranous. *Produced leaf* linear to terete with adaxial groove usually present, exceeding the inflorescence; leaf inserted above ground level, rarely more than halfway up the stem. *Bract leaves* 1–4, 2.5–6 cm long, herbaceous with dry, brown, acute apex. *Scape* usually erect and bearing to 8 branches; branches held erect, upper part held away from axis. *Inflorescence*

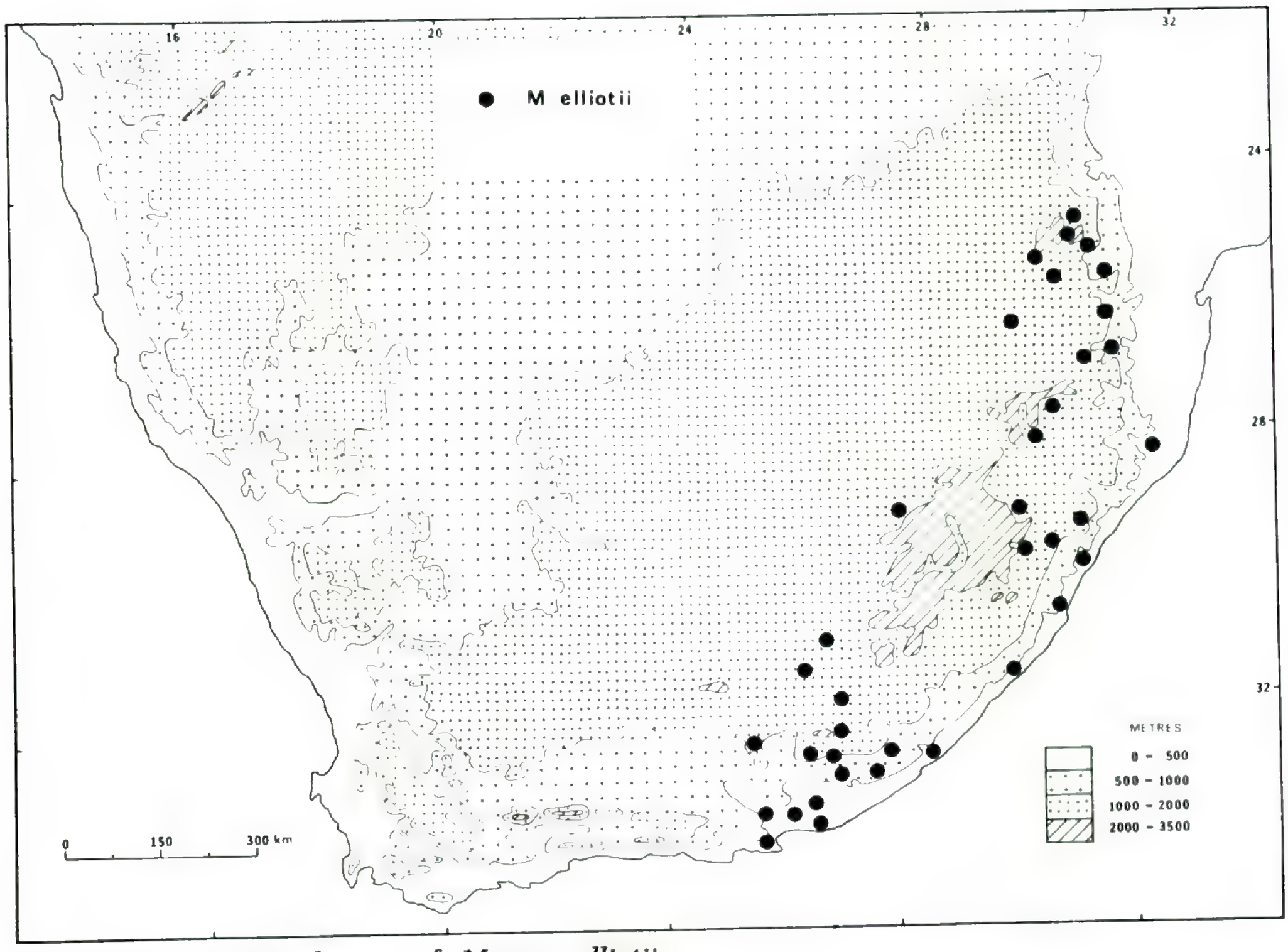

FIGURE 5. Distribution of *Moraea elliotii*.

spathe to 6 cm long, usually about 4.5 cm; inner spathe herbaceous, with a brown membranous apex and margin; outer spathe shorter than inner by 1 cm, frequently brown almost to the base. *Flowers* blue to violet with orange-yellow nectar guides; *outer perianth segments* 2–3 cm long, limb to 1.5 cm long and to 1.2 cm broad; *inner perianth segments* 1.5–2.4 cm long and 2–4 mm wide, linear-lanceolate. *Stamens* joined at base. *Style* branching near base, branches about 1 cm long, crests to 0.5 cm long. *Capsule* clavate, to 1.2 cm long and 0.4 cm wide; *seeds* small, angled. *Chromosome number* $2n = 12$, *Lewis 6306* (MO) as *M. setacea*; $= 24$, *Goldblatt 840* (BOL).

Flowering time: September to March, usually late spring in the south and summer to autumn in the north.

Distribution: Widespread, from the eastern Cape, throughout Natal and in Swaziland and the eastern Transvaal (Fig. 5).

Moraea elliotii is treated in the present paper in a very wide sense and several closely allied species have been reduced to synonymy. The type specimen and plants of other collections from the Transvaal highveld have a linear leaf inserted high up on the stem, but not immediately under the inflorescence as in *M. natalensis*. Specimens corresponding to *M. stewartae* tend also to have a linear leaf inserted above ground level, but the position of insertion is variable. A third species, *M. juncifolia*, also varies in the position of insertion of the leaf in the stem. The leaf in the latter species is terete or subterete. The three species mentioned above all occur in the Transvaal and Swaziland and generally flower from December to March.

Closely matching *Moraea juncifolia* with its terete leaf is *M. violacea*, the type from Byrne, Natal. Other specimens from the Natal midlands correspond to this form, and generally have the leaf inserted near groundlevel. The leaf varies from terete to linear. In Natal, plants generally flower in late spring. Further south in the eastern Cape, forms of *M. elliotii* flower earlier, from September onwards. In the eastern Cape forms corresponding to *M. macra*, leaf insertion is usually basal but the leaf may either be linear or terete.

The flowers and the corms of all the species now placed in *Moraea elliotii* are very similar, the former being small and blue with yellow-orange nectar guides. Branching is variable and though it can generally be said that the northern forms are fewer branched, many exceptions occur.

It was originally believed by the author that *Moraea elliotii* could be divided into subspecies or even two separate species, but no consistent differences could be found between the southern, somewhat smaller, more branched forms with a basal leaf insertion and the northern forms which are usually larger, less branched, and have a variable position of leaf insertion.

Moraea elliotii is most closely related to *M. stricta*, but this is an early flowering species which is easily distinguished by the absence of a green leaf when it is in flower. The forms of *M. elliotii* with the leaf inserted high on the stem can be confused with *M. natalensis*, but the latter is a more slender plant with very small flowers, and the leaf is inserted at the base of the inflorescence. *Moraea elliotii* is frequently confused in herbaria with *M. setacea*, which is actually a species of *Gynandriris*. The cause of the mistaken determinations is not clear.

24.30 (Pilgrim's Rest): Black Hill, Pilgrim's Rest (-DC), *Galpin 14326* (BOL, PRE).

25.30 (Lydenburg): Dullstroom (-AC), *Galpin 13070* (BOL, PRE); *Noome s. n.* (PRE 20796); Mount Anderson (-BA), *Mauve 4903* (PRE); near Sabie (-BB), *Brent 103* (PRE); Devils Knuckles, *Wilms 1418* (P); near Waterval Boven (-CB), *Reynolds 2311* (PRE).

25.31 (Komatipoort): Golden Crescent Mountain (-C), *Galpin 859* (PRE, SAM).

26.29 (Bethal): Spitskop, Ermelo (-BD), *Pott s. n.* (PRE 15143).

26.30 (Carolina): Mooi Hoek (-DD), *Devenish 305* (PRE).

26.31 (Mbabane): Ukutula, Mbabane (-A), *Compton 24808* (NBG); Mbabane (-AC), *Burtt-Davy 2870* (BOL); Hlatikulu (-CD), *Compton 29504* (PRE), *Stewart s. n.* (PRE, SAM 2534).

27.30 (Vryheid): Naauwhoek district (-CB), *Devenish 1103* (PRE).

28.30 (Dundee): Dundee townlands (-AA), *Shirley s. n.* (NU 32312); Mpati Mountain, Dundee district, *Shirley s. n.* (NU 32328); Dundee airfield, *Shirley 119* (NU).

28.32 (Mtubatuba): Dukuduku (-AC), *Strey 5535* (NH); St. Lucia, *Louw 1948* (PRE).

29.27 (Maseru): Mamathes (-BB), *Jacot-Guillarmod 3008* (PRE).

29.29 (Underberg): Estcourt Plant Research Station (-BB), *Acocks 10756* (PRE); hills near Ladysmith (-DB), *Wood s. n.* (NH 4989).

29.30 (Pietermaritzburg): Noodsberg (-BD), *Ward 946* (NU); Oribi airfield (-CB), *Brayshaw 69* (NU); Merebank East, Durban (-DD), *Ward 5213* (NH, NU, PRE); Clairmont, *Wood 11580* (NH); near Umbilo, *Wood s. n.* (NH 20809); near Durban, *Wood 4943* (PRE).

30.26 (Aliwal North): Elands Hoek, Aliwal North (-DC), *F. Bolus 130* (BOL).

30.30 (Port Shepstone): Park Rynie (-BC), *Shepherd 14* (NH); Ifafa, *Handley 48* (NU).

31.26 (Queenstown); North of Molteno (-AD), *Theron 923* (PRE); Queenstown range (-DD), *Galpin 2193* (BOL, PRE).

31.29 (Port St. Johns); Port Grosvenor (-BD), *Strey 8877* (NH).

32.25 (Somerset East): Jakkalsfontein, Cradock, *Acocks 17515* (PRE).

32.26 (Fort Beaufort): South of Gardiners Drift (-BD), *Acocks 20110* (NBG, PRE);

Black Hill, Lovedale (-CB), *Barker 2768* (NBG); Gaikas Kop, Amatola mountains (-DB), *Grant 3082* (BOL); Alice (-DD), *Goldblatt 840* (BOL), *Barker 2181* (NBG).

32.27 (Stutterheim): Emtaleni, Kei road, *Ranger 407* (PRE); near Komgha (-DB), *Flanagan 786* (PRE, SAM); Berlin (-DC), *Marais 446* (PRE).

32.28 (Butterworth): Near Kei River mouth (-CB), *Flanagan 1814* (BOL, SAM).

33.25 (Port Elizabeth): Addo Park (-BC), *Liebenberg 6614* (PRE); Port Elizabeth (-DC), *Burtt-Davy 12023* (PRE).

33.26 (Grahamstown): Howison's Poort (-AD), *H. M. L. Bolus 14465* (BOL); Grahamstown (-BC), *Schonland 1506* (BOL); *Rogers 1535* (PRE); Bushman's River mouth (-DA), *Barker 1334* (NBG).

4. **Moraea natalensis** Baker, Handbook Irid. 56. 1892. Types: Natal, *Sanderson 253* (K, lectotype, S, isolectotype) and *Sutherland s. n.* (K).

Moraea parviflora N. E. Br., Trans. Roy. Soc. S. Africa 17: 346. 1929. Type: Tomson's vlei, Nylstroom, *Pole-Evans 19668* (K, holotype, PRE, isotype).

Plants 15–45 cm in height including leaf. *Corm* to 1.5 cm diameter, covered with tunics of dark brown to black fibres. *Prophyll* membranous reaching a few cm above ground. *Produced leaf* inserted high up on stem, just below inflorescence; at time of flowering shorter, more often overtopping the inflorescence, to 20 cm long, narrowly canaliculate to terete. *Stem* green, erect or leaning over, lowermost internode very long with the leaf inserted above it, remainder of stem much shorter, flexuously branched, rarely simple. *Bract leaves*, if present, seldom more than 2.5 cm long, usually dry, light brown. *Inflorescence* 2.5–3.5 cm long and 2–3 mm thick; inner spathe herbaceous with dry apex and margin, to 1 cm longer than outer; outer spathe dry, brown near apex, often lacerated, speckled lower down. *Flowers* lilac to mauve with yellow nectar guide ringed with dark mauve; *outer perianth segments* about 1.4–2 cm long, limb 7–14 mm long and to 10 mm wide, claw fairly narrow; *inner perianth segments* linear-lanceolate, to 1.5 cm long and 4 mm wide. *Stamens* branching almost at base, branches to 11 mm including crests, pressed against claw of outer segment. *Capsule* ovoid to clavate, 4.5–10 mm long and to 4 mm wide. *Seeds* angled.

Flowering time: Summer.

Distribution: Coastal to mid-altitudes in Natal and Transvaal (Fig. 6).

There is some variation in the species as circumscribed here. The type form occurs in Natal in the Pietermaritzburg area. Further north in the Transvaal, a slender form with a smaller capsule is found as typified by *Moraea parviflora* N. E. Br. from Nylstroom. Some plants from the area are much branched, but others resemble the Natal plants in having only a few branches. *Moraea parviflora* is reduced to synonymy here as there seems no justification for maintaining it as distinct.

Moraea natalensis is clearly allied to *M. inclinata* as can be seen from the similar habit with the leaf insertion high on the stem. The overall smaller size, in flowers as well as vegetative parts, and the differences in bracts, spathes and capsules do, however, make it easy to distinguish the two. The central African species *M. ericirosenii* Fries is allied to *M. natalensis*, and the relationship between these two species requires investigation.

24.28 (Nylstroom): Tomsons vlei, Nylstroom, *Pole-Evans s. n.* (PRE 19668); Geelhoutkop (-AD), *Breyer s. n.* (PRE 31518); Nylstroom (-CD), *van Dam s. n.* (PRE 9654).

24.30 (Pilgrim's Rest): Mac Mac Falls (-DD), *Almborn 744* (LD).

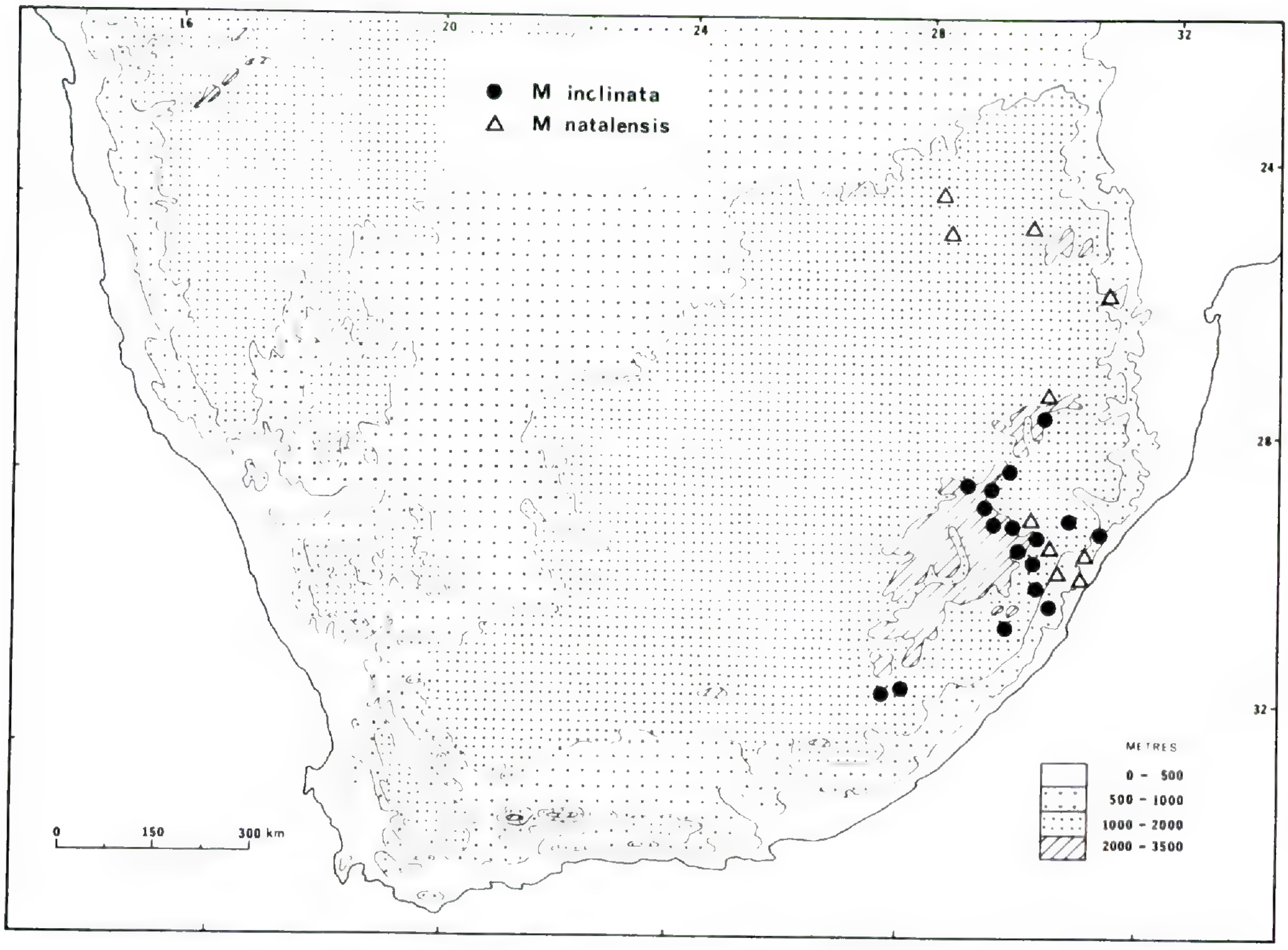

FIGURE 6. Distribution of *Moraea natalensis* and *M. inclinata*.

25.31 (Komatipoort): Barberton (-CC), *Pott 5461* (PRE).
27.30 (Vryheid): Oshoek, near vlei (-AC), *Mauve 4497* (PRE).
29.29 (Underberg): Estcourt Plant Research Station (-BB), *Acocks 10756* (PRE).
29.30 (Pietermaritzburg): Howick (-AC), *Rycroft 2067* (BOL); Lidgetton, *Mogg 770* (PRE); Richmond road (-CD), *Barker 4375* (BOL); Arnolds Hill, Richmond, *Wylie s. n.* (NH 23372); between Bisley and Richmond, *Almborn 846* (LD); Groenberg (-DB), *Wood 1072* (SAM, PRE); Umbilo (DD), *Wood 520* (BOL).

5. **Moraea inclinata** Goldbl., sp. nov. Type: Cathkin Park, *Galpin 11847* (BOL, holotype, PRE, isotype).—FIG. 3F.

Planta gracilis, ad 90 cm alta. *Cormus* 1–1.5 cm diam., tunicis atrobrunneis. *Prophylla* fibrosa. *Folium* insertum ad basem inflorescentiae, 15–40 cm longum, lineare, canaliculatum aut teres. *Folia vaginantia* 1–2 cm longa, pallida-brunnea. *Scapus* gracilis, glaber aut lanuginosus, plerumque inclinatus ad terram, simplex an pauciramosus. *Inflorescentia* 2.5–4 cm longa, spatha exterior brevior dimidio quam interior, brunnea aut viridis sole ad basem. *Flores* caerulei, lutea nota; *perianthii segmenta exteriora* 2.5–3 cm longa, 1 cm lata, limbi reflexi; *segmenta interiora* 2–2.5 cm longa, ad 6 mm lata, limbi reflexi. *Filamenta* connata ad basem, 5 mm longa, *antherae* circa 7 mm longae. *Stylus* ad 5 mm longus, rami 6 mm longi cristae ad 5 mm longae. *Germen* clavatum; capsula sphaerica, ad 6 mm diam. *Semina* angulata.

Plant fairly tall, 40–90 cm long including the leaf. *Corm* 1–1.5 cm in diameter, with tunics of brown fibres sometimes extending upwards in a neck. *Prophylls* covering the underground part of the stem. *Produced leaf* inserted high up on stem, just below the inflorescence, usually between 15–40 cm long, canaliculate, to 3 mm wide or terete with margins inrolled. *Scape* slender, glabrous or rarely woolly, usually leaning to one side, bearing a long leaf towards the apex, just

below the inflorescence; usually flexed and branched above the leaf and bearing to 4 flower clusters. *Bract leaves* 1–2 cm long sheathing the stem, with apex free, dry and light brown, or base only green. *Inflorescence* several flowered; 2.5–4 cm long and up to 4 mm thick, inner spathe with a membranous dry speckled margin and brown tip; outer spathe much shorter, rarely half the length of inner; dry, light brown or green at base only. *Flowers* blue with yellow nectar guide on outer petals; *outer perianth segments* 2.5–3 cm long and 1 cm wide at broadest point, both limb and claw fairly broad, limbs reflexed; *inner perianth segments* 2–2.5 cm long and up to 6 mm wide, limbs reflexed. *Filaments* connate at base, up to 5 mm long, anthers 7 mm long. *Style* branching about 5 mm from base, branches about 6 mm long and up to 3 mm wide, style crests up to 5 mm long. *Ovary* clavate, capsule spherical, up to 6 mm in diameter. *Seeds* angular.

Flowering time: Late spring to early summer.

Distribution: Slopes of the Drakensberg in Natal and the north eastern Cape (Fig. 6).

Icon: Trauseld, Wild Flowers of the Natal Drakensberg. 35, *fig. 162.* 1969.

Although *Moraea inclinata* is a quite distinct species, it has in the past been confused with *Moraea natalensis* which has a similar habit with the leaf inserted on the stem just below the inflorescence. An examination of large numbers of plants has indicated that two species are involved. *Moraea natalensis* is a smaller, more slender plant found in both the Transvaal and in Natal where its distribution borders on that of *M. inclinata* along the foothills of the Drakensberg. The two can easily be distinguished by the capsules, which are spherical in *M. inclinata* and ovoid in *M. natalensis.* The size of the spathe bracts and flowers are also quite distinct features.

27.30 (Vryheid): Zwartkop (-CB), *Wood 10233* (NH).
28.28 (Bethlehem): Mont aux Sources area (-DB), *Trauseld 162* (PRE); Tiger Cave Valley, *Evans 493* (NH).
28.29 (Harrismith): Near Oliviers Hoek (-CA), *Wood 3442* (NH); Cathedral Peak area (-CC), *Killick 1260* (NH).
28.30 (Dundee): Weenen district (-CC), *Wood s. n.* (BOL 30815).
29.29 (Underberg): Giants Castle Game Reserve (-AB), *Bruyns-Haylett 13* (NU); *Trauseld 977* (NU); *Symons 307* (PRE); Cathkin Park, Little Berg, *Galpin 11847* (BOL, PRE); Estcourt (-BB), *Plowes 2392* (NH, PRE); Ross, Umgeni Poort (-BD), *Moll 1427* (NU).
29.30 (Pietermaritzburg): Cleveland farm (-AC), *Smuts 1411* (PRE); Balgowan, *Moll 2854* (PRE); near Curry's Post, *Wood 3436* (NH); Greytown (-BA), *Wylie s. n.* (NH 21726); Dargle (-CA), *Hilliard and Burtt 3192* (NU); Mountain Glen, Dargle, *Taat 1317* (PRE); Liddesdale, *Wood 4255* (NH).
29.31 (Stanger): Ensikeni (-AC), *Haygarth sub Wood 12079* (BOL, NH).
30.29 (Kokstad): Weza-Ngeli slopes (-DA), *Strey 6279* (NH, NU, PRE).
30.30 (Port Shepstone): Ixopo district (-AA), *Shirley s. n.* (NU 32366); Dumisa near Ifafa (-AD), *Rudatis 432* (PRE).
31.27 (Lady Frere): Little Bush, Cala, *Pegler 1702* (LD); Kwenkwe Mountain, Maclear district (-DA), *H. Bolus 8714* (BOL); Engcobo mountains (-DB), *H. Bolus 10308* (BOL); *Flanagan 2661* (PRE, SAM).
Doubtful locality: Drakensberg summit, *Wood 3442* (BOL).

6. **Moraea stricta** Bak., Viert. Nat. Ges. Zürich 49: 178. 1904. Type: Shilouvane, Tvl. *Junod 563* (Z, holotype, K, LD, isotypes).

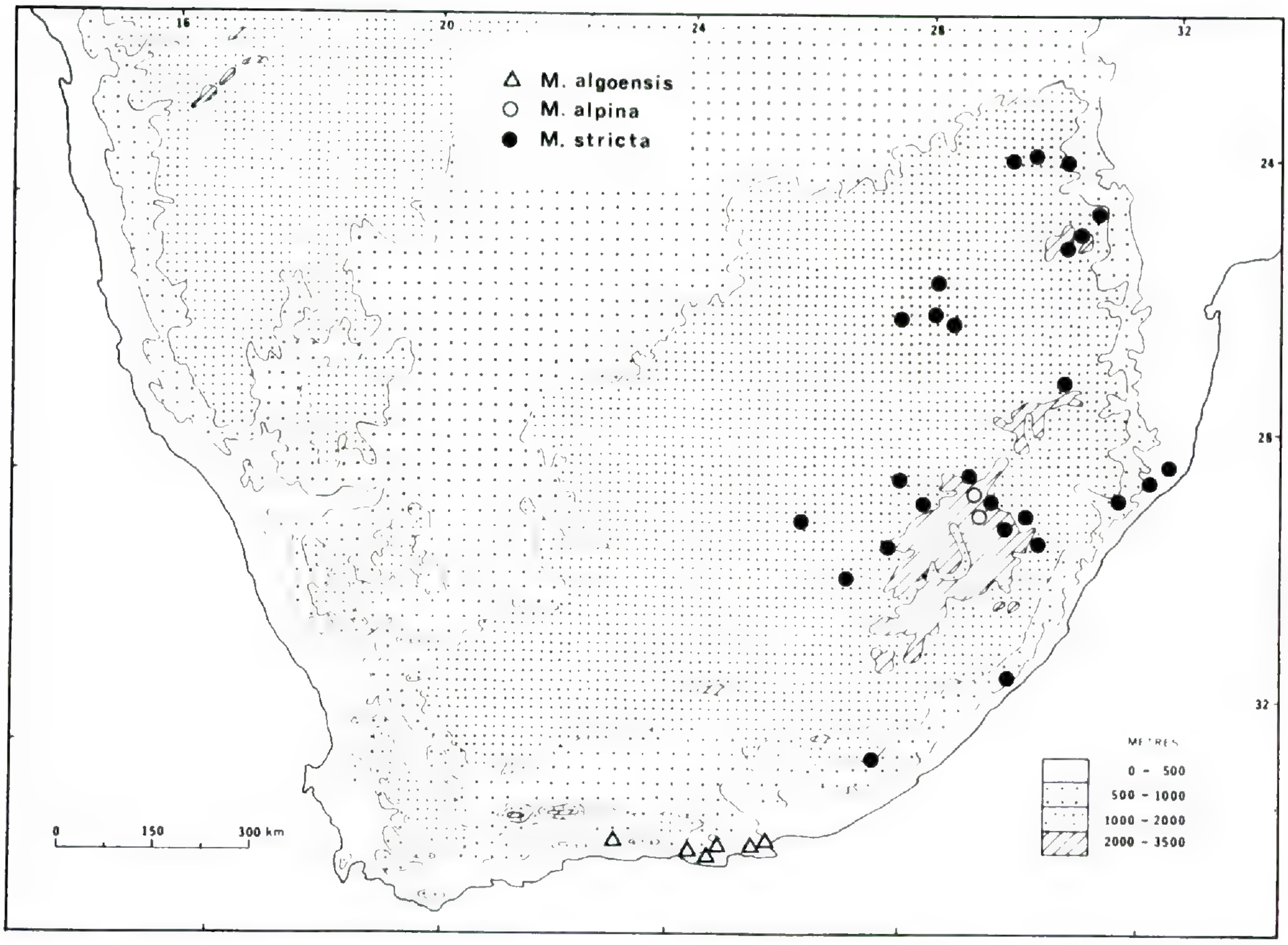

FIGURE 7. Distribution of *Moraea stricta*, *M. alpina*, and *M. algoensis*.

Moraea trita N. E. Br., Trans. Roy. Soc. S. Africa 17: 347. 1929. Type: Lydenburg, *Wilms 1419* (K, holotype, P, PRE, isotypes).
Moraea parva N. E. Br., Trans. Roy. Soc. S. Africa 17: 347. 1929. Type: Woodbush, *Moss 15564* (K, holotype).
Moraea mossii N. E. Br., Trans. Roy. Soc. S. Africa 17: 347. 1929. Type: Johannesburg, *Moss 15805* (K, holotype, PRE, isotype).

Plants small to medium, usually 15–25 cm high. *Corm* 1–3 cm in diameter, tunics of medium to coarse fibres, dark brown in color, often bearing cormlets among the fibres. *Basal leaf* usually absent at flowering time (or dead and still attached to base of scape), occasionally new leaf emerging; eventually produced to about 60 cm or more, about 1.5 mm thick, terete, without adaxial groove. *Sheathing leaves* brown, membranous, covering underground part of scape and new leaf. *Bract leaves* 3–6 cm long, dry, membranous, brown; apices often lacerated. *Scape* erect, usually bearing 3–6 branches; branches held close to main stem, on short peduncles or sessile. *Inflorescence* several flowered, 3–4 cm long; spathe bracts dry and papery, rarely green near the base, apices membranous, speckled darker brown, sometimes lacerated; inner bracts larger but almost equal in length to outer, sometimes shorter. *Flowers* pale lilac to mauve with yellow spotting on outer petals; *outer perianth segments* about 2 cm long, limb about 1 cm long and 4–7 mm wide, obovate to lanceolate, *inner perianth segments* slender, erect, about 1.5–1.8 cm long and 2–4 mm wide, linear-lanceolate. *Stamens* connate at base only, filaments about 3.5 mm long, anthers 5 mm long. *Style* branching about 1.5 mm from base, branches 7–8 mm long, crests lanceolate,

3 mm long. *Ovary* clavate; *capsule* 1 cm × 0.5 cm. *Seeds* small, yellow, angled. *Chromosome number*: $2n = 24$, *Goldblatt 155* (J).

Flowering time: July to November.

Distribution: Occurring in grasslands from the eastern Cape to the northern Transvaal (Fig. 7).

Icon: Letty, Wild Flowers of the Transvaal. *Pl. 36, fig. 1.* 1962.

Moraea stricta is a very distinct species and is easily recognised by the very characteristic lack of a green leaf at flowering time. The previous season's dead, dry leaf is sometimes attached to the flowering stem, and its presence often gives rise to confusion over identification, especially in the case of herbarium material. The branches hugging the main axis and the dry bracts are, however, also characteristic and should aid determination.

Moraea stricta has been known as *M. trita* since N. E. Brown described the latter species in 1929. An examination of the description and type of *M. stricta* Baker has, however, revealed that it is an earlier name for this plant. Two other species *M. parva* and *M. mossii* described by N. E. Brown also appear, to the present author, to be synonyms of *M. stricta*.

23.29 (Pietersburg): Pietersburg (-CD), *Wilkinson s. n.* (PRE 31516); near Haenertsburg (-DD), *Burtt-Davy s. n.* (BOL 4119); *Zeederberg s. n.* (PRE 4087).
23.30 (Tzaneen): Letaba (-CD), *Scheepers 1164* (PRE).
24.30 (Pilgrim's Rest): Near Belvedere (-DB), *Davidson 621* (J).
25.28 (Pretoria): Lynnwood (-CA), *Letty 381* (PRE).
25.30 (Lydenburg): Lydenburg (-AB), *Wilms 1419* (PRE); near Lydenburg (-BA), *Wilms 1418* (P).
26.27 (Potchefstroom): Krugersdorp (-BB), *Bush s. n.* (PRE 8171); Witpoortjie Kloof, *Moss 8013* (J).
26.28 (Johannesburg): Thorntree Kloof, *Moss 15956* (PRE); Johannesburg (-AA), *Moss 2877, 15805* (both PRE); Milner Park, Johannesburg, *Moss 18199* (PRE); Houghton Ridge, Johannesburg *Moss 2879* (PRE); Melville Koppies, *Goldblatt 155* (J); Benoni (-AB), *Bradfield 91* (PRE).
27.30 (Vryheid): Oshoek, Wakkerstroom district (-AC), *Devenish 1153* (PRE).
28.27 (Senekal): Strathcona, Ficksburg district, *Galpin s. n.* (BOL 30813); Moolmans Hoek Peak, *Galpin s. n.* (BOL 30814).
28.28 (Bethlehem): Leribe (-CC), *Dieterlen 324* (NH); Mont aux Sources (-DB), *Hutchinson, Forbes & Verdoorn 122* (NH, PRE).
28.29 (Harrismith): Cathedral Peak area (-CC), *Esterhuysen 12895* (BOL).
28.31 (Nkandla): Eshowe (-CD), *Lawn 911* (NH); *Gerstner s. n.* (NH 22960); Empangeni district (-DB), *Venter 1987* (NH).
28.32 (Mtubatuba): Lower Umfolosi area, *Hitchins 44* (NU, PRE).
29.26 (Bloemfontein): Bloemfontein (-AA), *Potts s. n.* (PRE 2867); Erasmus (-DD), *Repton 450* (PRE).
29.27 (Maseru): Roma (-BC), *Ruch 20* (PRE).
29.28 (Marakabei): Maletsunyani Falls (-CC), *Esterhuysen 13185* (BOL); M'weni area, *Esterhuysen 18686* (BOL).
29.29 (Underberg): Cathkin area (-AB), *Esterhuysen 7941* (BOL); Giants Castle Game Reserve, *Trauseld 1012* (NU, PRE); *Skead 173* (NU); near Mooi River (-BB), *Schlechter 3331* (BOL); Estcourt district *West 814* (PRE).
29.30 (Pietermaritzburg): Nottingham road (-AC), *Levett 6* (NH).
31.29 (Port St. Johns): Port St. Johns area (-DA), *Baker 9, 11* (PRE).
32.27 (Stutterheim): Stutterheim commonage (-CB), *Acocks 9125* (PRE).

7. **Moraea alpina** Goldbl., sp. nov. Type: Mont aux Sources, *Galpin 10361* (PRE, holotype).

Planta parva, 4–12 cm alta. *Cormus* circa 0.7 cm diam., tunicis fibris pallidis. *Prophylla* membranacea. *Folium basale* gracile teres, 0.5 mm diam., abscens aut emergens tempore florendi, si emergens nunc non insertum in caule florenti. *Folia vaginantia* sicca, membranacea, 5–15 mm longa. *Scapus* contractus, simplex aut pauciramosus. *Inflorescentia* pauciflora circa 2.5 cm longa, 3 mm lata, spatha viridis, marginibus hyalinis, interior quam exteriorem excedens 1 cm. *Flores* atrocaerulei aut violacei, lutea nota; *perianthii segmenta exteriora* ad 1.2 cm longa, 3–4 mm lata; *segmenta interiora* breviora, apicibus aliquot expansis. *Filamenta* connata ad basem, anthere 3 mm longae. *Stylus* ramosus prope basem, rami 6 mm longi, cristae 1.5 mm longae. *Germen* clavatum, capsula sphaerico-ovoidea, ad 5 mm longa. *Semina* angulata.

Plants very small, 4–12 cm high. *Corm* about 0.7 cm in diameter with tunics of fine, light brown fibres. *Prophylls* membranous, covering lower portion of leaf and scape. *Basal leaf* slender, terete, 0.5 mm in diameter, absent or emergent at time of flowering; not attached to flowering stem but to corm. *Bract leaves* dry and membranous, 5–15 mm long. *Scape* slender, few-branched or simple; contracted. *Inflorescence* several-flowered, about 2.5 cm long and 3 mm thick; spathes green, margin hyaline, inner exceeding outer by about 1 cm. *Flowers* dark blue to violet with yellow nectar guides; *outer perianth segments* about 1.2 cm long and 3–4 mm wide; *inner perianth segments* shorter than outer, somewhat expanded near apex. *Filaments* joined near base only, anthers 3 mm long, exceeding the stigmas. *Style* branched almost from base, branches 6 mm long, style crests 1.5 mm long. *Ovary* clavate; capsule spherical to ovoid, to 5 mm long. *Seeds* angular.

Flowering time: December.

Distribution: Summit plateau of the Drakensberg in Natal and Lesotho (Fig. 7).

Moraea alpina is a very poorly known species which, although collected only twice, seems quite distinct. Its most remarkable feature is its small size, which may account for its infrequent collection. The terete structure of the basal leaf and the fact that it is not attached to the flowering stem of the same season, indicate a relationship with *M. stricta*, a large spring flowering species which is leafless when in bloom. Other features such as the short length and thickness of the inflorescences, the rotund shape of the capsule and the length of bract leaves suggest it is not a diminutive, late flowering form of *M. stricta*, but a distinct species, though probably closely related to its postulated ally. It is of interest to note that *M. stricta* occurring in the same area of the Drakensberg flowers much earlier (September or October) even at high altitudes.

28.28 (Bethlehem): Beacon Buttress, summit (-DD), *Galpin 10367* (PRE).
28.29 (Harrismith): Cleft Peak area (-CC), *Killick & Marais 2182* (PRE).

8. **Moraea algoensis** Goldbl., sp. nov. Type: Port Elizabeth, *Batten 7* (NBG, holotype).—FIG. 3G.

Planta 20–30 cm alta. *Cormus* ad 1 cm diam. *Prophylla* membranacea. *Folium basale* lineare, canaliculatum, 2–3 mm latum, inflorescentiam excedens. *Folia vaginantia* ad 4 cm longa, sicca et brunnea supra, apicibus acutis. *Scapus* ramosus, rami 2–4, saepe secundi. *Inflorescentia* ad 5 cm longa, spatha exterior breviore prope dimidio, apicibus acutis, marginibus brunneis et membranaceis. *Flores* atrocaerulei, lutea nota; *perianthii segmenta exteriora* ad 2.6 cm longa; limbus ad 1.6 cm longus et ad 9 mm latus; *segmenta interiora* brunnea, breves, 6–10 mm longa; limbus expansus, ad 2.5 mm latus. *Filamenta* 4 mm longa, connata ad 3 mm, antherae circa 4 mm longae. *Stylus* 4 mm longus, rami 5 mm longi, cristae lineares, ad 8 mm longae. *Germen* clavatum, seminibus angulatis.

Plants 20–30 cm in height. *Corm* about 1 cm in diameter. *Prophylls* reaching to ground level. *Basal leaf* linear, inserted near ground level, canaliculate, 2–3 mm wide, terete when dry, exceeding the inflorescence. *Bract leaves* to 4 cm long, dry and brown in upper part with long tapering apex. *Scape* branched, branches 2–4 held away from axis, often all facing to one side. *Inflorescence* to 5 cm long, outer spathe about half length of inner; both spathe bracts with brown membranous margin and tapering apex. *Flowers* dark blue with yellow nectar guide; *outer perianth segments* to 2.6 cm long, limb about 1.6 cm long and about 0.9 cm broad; *inner perianth segments* brown, comparatively short, 6–10 mm long, reaching to about the level of the stigmas, distinctly unguiculate, limb expanded, ovate, to 2.5 mm broad. *Filaments* joined for 3 mm, filaments free for 1 mm, anthers about 4 mm, not reaching the stigmas. *Style* column about 4 mm, branches 5 mm, crest linear up to 8 mm long. *Ovary* clavate. *Seeds* angled.

Flowering time: July to September.

Distribution: Southern Cape in the Port Elizabeth–Humansdorp area (Fig. 7).

Icon: Batten and Bokelmann, Wild Flowers of the Eastern Cape Province. 27, *fig.* 7. 1966.

Moraea algoensis, which occurs on the borders of the summer and winter rainfall areas, appears to be distinct from its allies *M. elliotii* and *M. tripetala*. Its very characteristic feature is the inner perianth segment which is brown, and, although comparatively short, has a broad expanded limb. The species has, until now, been undescribed although it has been known for many years.

33.23 (Willowmore): Between Knysna and Avontuur (-CC), *Fries, Norlindh & Weimarck 1790* (SAM).

33.24 (Steytlerville): Assegaibosch (-CD), *Fourcade 1427* (BOL); 70 km W of Port Elizabeth (-DD), *Story 2834* (PRE).

33.25 (Port Elizabeth): Witteklip flats (-CC), *Holland s. n.* (BOL 30812); Port Elizabeth (-DC), *Hafstrom & Acocks s. n.* (PRE 31513); Redhouse *Paterson 439* (BOL); near Port Elizabeth, *West 311* (BOL); *Batten 7* (NBG).

34.24 (Humansdorp): Humansdorp (-BB), *Loubser 880* (NBG).

Group IV: Vieusseuxia

9. **Moraea pubiflora** N. E. Br., Trans. Roy. Soc. S. Africa 17: 348. 1929. Type: Hlatikulu, Swaziland, *Miss Stewart s. n.* (K, holotype, PRE, isotype).

Plants of medium height, seldom exceeding 60 cm. *Corm* to 2 cm in diameter, covered with tunics of dark brown netted fibres, sometimes forming a neck. *Prophyll* pale to dark brown, ribbed below. *Leaf* inserted near base, above ground level, linear canaliculate, about 4 mm wide and up to 60 cm long. *Bract leaves* 2–3, green, with dry brown apex, 5–8 cm long. *Scape*, usually branched, bearing to 10 branches, all held to one side, close to axis. *Inflorescence* several flowered, spathe bracts green, with dry apex, inner to 8 cm, outer about half the length of inner. *Flowers* white to pale blue or lilac; *outer perianth segments* to 3 cm long, limb about 1.5 cm long spreading, lanceolate, claw bearded on inner surface, scabrid or smooth on outer surface; *inner segments* trifid, green spotted with brown; outer lobes slender, 4–8 cm long, obtuse, erect; inner lobe linear,

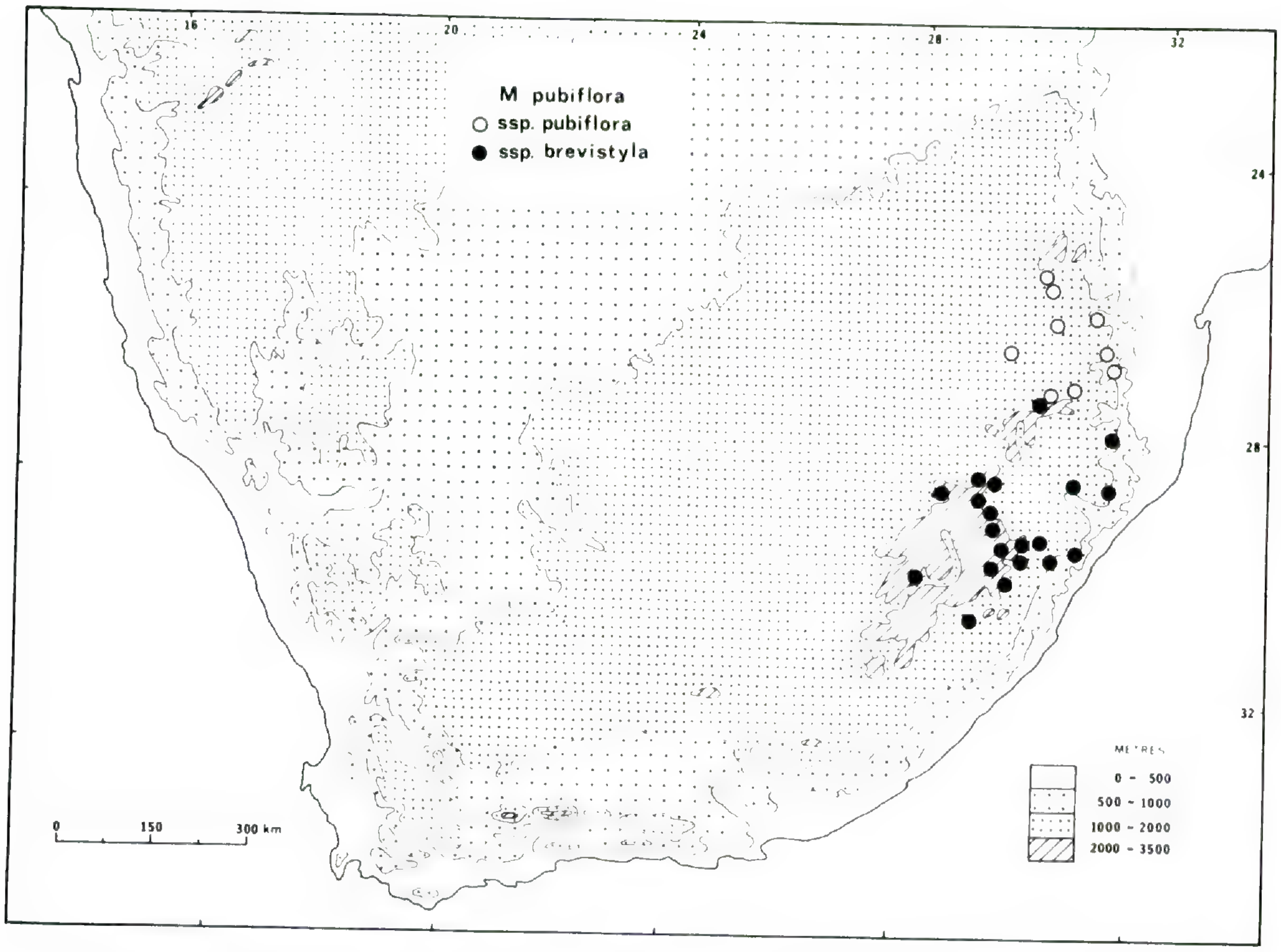

FIGURE 8. Distribution of *Moraea pubiflora* subsp. *pubiflora* and subsp. *brevistyla*.

acute, curving outwards, 4–8 cm long. *Filaments* to 1.5 cm long, free near apex only; *anthers* 4–6 mm long extending beyond the stigmas. *Style* to 1.5 cm long, branches 4 mm long, crests linear, 3–4 mm long. *Ovary* clavate; *capsule* barrel-shaped, to 1 cm long.

Flowering time: Summer.

Distribution: Grasslands in the eastern Cape to the south eastern Transvaal and Swaziland (Fig. 8).

Icon: Trauseld, Wild Flowers of the Natal Drakensberg. 37, *fig.* 325. 1969.

This species can easily be recognised by the peculiar structure of the inner perianth segments, which are divided into 3 subequal slender lobes, the outer two being expanded at the apex and obtuse, and the inner slender with an acute apex (Fig. 3D). Such a structure also occurs in some forms of *Moraea dracomontana*, an allied species from the Drakensberg. Here, however, the inner segments appear uniformly purple, while those of *M. pubiflora* are mottled brown and yellow. Other differences in size, branching habit, and habitat make it unlikely that these two be confused. The structure and flower color of *M. tenuis* from the winter rainfall area are remarkably similar to *M. pubiflora*, especially subsp. *brevistyla* and indicate a close relationship. *Moraea pubiflora* is treated as comprising two subspecies: the northern form with a robust habit, large flowers with a markedly scabrid outer surface on the claw of the outer petals and a long style and filament column; and the southern, with smaller flowers, little or no scabridity and a short style and filament column.

KEY TO THE SUBSPECIES

1. Filaments 1–1.2 cm long ..... 9a. subsp. *M. pubiflora*
1′. Filaments 0.5–0.7 cm long ..... 9b. subsp. *M. brevistyla*

9a. subsp. **pubiflora**

Plants generally more robust than in subsp. *brevistyla*, bearing 2 or 3 (rarely to 6) branches. *Flowers* large, with outer segments to 3 cm long; claw to 1.5 cm, outer surface markedly scabrid to pubescent. *Filaments* to 1.5 cm long. *Style* to 1.2 cm long, branches to 4 mm.

Distribution: South eastern Transvaal and Swaziland (Fig. 8).

This subspecies can easily be recognised by the length of the style and filament column which is about 1–1.2 cm long. In addition subsp. *pubiflora* usually bears fewer branches and has larger flowers which exhibit the unusual character of scabridity or pubescence on the outer surface of the outer perianth segments.

25.30 (Lydenburg): Dullstroom (-AC), *Noome 20798* (PRE); *Galpin s. n.* (BOL); Belfast (-CA), *Leendertz s. n.* (PRE 9168); *H. Bolus 12332* (BOL, PRE).

26.29 (Ermelo): Ermelo common (-DB), *Sisters of Ermelo Convent 17* (PRE).

26.31 (Mbabane): Forbes Reef (-AA), *Karsten s. n.* (BOL 57876, PRE 31515); Stroma, Mbabane (-C), *Compton 24830* (NBG); Mankaiana (-CA), *Compton 25311* (NBG, PRE); Hlatikulu (-CD), *Stewart s. n.* (K, PRE 9551); *Compton 26376* (NBG).

27.30 (Vryheid): Tafelkop, Wakkerstroom (-AC), *Mauve & Tolken 4528* (PRE); Mooi Hoek, near vlei (-BA), *Devenish 312* (PRE).

Doubtful locality: Stafford, Ermelo district, *du Plessis 101* (PRE); near Olifants River, *Schlechter 4023* (BOL).

9b. subsp. **brevistyla** Goldbl., subsp. nov. Type: Cathkin Park, *Galpin s. n.* (BOL 30823, holotype).—FIG. 3D.

Planta parvior quam subsp. *pubiflora*, et plerumque plus ramosa. *Flores* parviores; *perianthii segmenta exteriora* ad 2 cm longa, unguis ad 6 mm longus; pagina exterior laevis an pubescens. *Filamenta* ad 7 mm longa. *Stylus* 6 mm longus, rami ad 4 mm longi.

Plants smaller than subsp. *pubiflora*, and usually bearing more branches, about 5 being average. *Flowers* smaller, with outer segments to 2 cm long; claw to 6 mm, outer surface lightly pubescent or smooth. *Filaments* to 7 mm. *Style* 6 mm long, branches to 4 mm.

Distribution: Occurring in the southern part of the range for *M. pubiflora*, from northern Natal to the Transkei (Fig. 8).

This subspecies can almost always be easily distinguished from subsp. *pubiflora* by its short style and filaments, and also by the lack of scabridity or pubescence on the reverse surface of the outer perianth segments so typical of subsp. *pubiflora*. The distribution of the two subspecies overlaps to some extent in the Wakkerstroom area on the Natal–Transvaal border, and both have been recorded here. Occasionally both lengths of stigma occur in one collection (*Mauve & Tolken 4528*), which suggested to the present author that subspecies and not separate species were involved. The southern, short-styled form was, however, regarded as a distinct taxon as the abrupt variation in style and filament lengths cannot be regarded as a cline, and such a difference in the reproductive organs is undoubtedly significant.

27.30 (Vryheid): South Hill, Wakkerstroom (-AC), *Galpin 9885* (PRE); Oshoek, Wakkerstroom, *Devenish 234* (PRE); Wakkerstroom, *Beeton 96* (SAM).
27.31 (Louwsburg): Ceza, Mahlabatini district (-CD), *Hilliard & Burtt 3320* (NU).
28.28 (Bethlehem): Mont aux Sources (-DA), *Flanagan 2037* (BOL, PRE, SAM); *Flanagan 2014* (BOL).
28.29 (Harrismith): Grootvlei near Swinburne (-AC), *Jacobsz 2* (PRE); Rensburgskop (-AD), *Jacobsz 6A* (PRE); van Reenen, *Franks s. n.* (NH 12159); Oliviershoek (-CA), *Strey 9508* (NH, PRE); Cathedral Peak area (-CC), *Schelpe 5380* (NU); *Schelpe 1300* (NU); Cathedral Peak Forest Reserve (-CD), *Killick 1282* (PRE).
28.30 (Dundee): Qudeni (-DB), *Gerstner 640* (PRE).
28.31 (Nkandla): Melmoth (-CB), *Mogg 6240* (PRE).
29.28 (Marakabei): Simonkong, Maletsunyane (-CC), *Esterhuysen 13186* (BOL).
29.29 (Underberg): Giants Castle Game Reserve (-AB), *Trauseld 3250* (CPF, NU, PRE); Cathkin Park, *Galpin s. n.* (BOL 30823); *Edwards s. n.* (BOL 30822); Giants Castle Game Reserve, *McKeown 80* (NU); Champagne Castle Hotel, *Acocks 10112* (NH); Highmoor Forestry Estate (-BC), *Smith 15* (NU); Nottingham Road (-BD), *Schweickerdt 1317* (PRE); Drayton *Smith 182* (NU); Umkomanza River valley (-CB), *Marais 1438* (PRE); Loteni Nature Reserve (-DA), *Killick 3849* (NH); Mahraqua mountains (-DC), *Evans 233* (NH).
29.30 (Pietermaritzburg): Ehlatini farm, Karkloof (-AC), *Moll 3484* (NH, PRE); Zwartkop (-CB), *Wood s. n.* (NH 11398); Inanda (-DB), *Wood 414* (NH); *Wood 1116* (NH, SAM).
30.29 (Kokstad): Mount Currie (-AD), *Edwards 950* (NU).

10. **Moraea albicuspa** Goldbl., sp. nov. Type: Source of the Tina River, summit of Drakensberg, *Galpin 6846* (BOL, holotype, PRE, SAM, isotypes).

Planta ad 60 cm alta. *Cormus* ad 2 cm diam., tunicis fibris brunneis. *Prophylla* brunnea, fracta irregulariter aut fibrosa. *Folium* canaliculatum, lineare, ad 40 cm longum. *Folia vaginantia* 3–4, 4–6 cm longa, virides, apicibus brunneis membranacea. *Scapus* erectus plerumque ramos 1–2 ferens. *Inflorescentia* 5–7 cm longa, spatha interior aliquantum longior exteriore. *Flores* albi-cremei, genu segmentarum exteriorum atromaculato; *perianthii segmenta exteriora* 3–3.5 cm longa, limbus 1.5–2 cm longus et ad 1.5 cm latus; *segmenta interiora* 5–7 mm longa, lineares, acuta. *Filamenta* ad 7 mm longa, libra sole ad apicem; *antherae* 5–6 mm longae, albae. *Stylus* ad 7 mm longus, rami 7 mm longi, cristae graciles, ad 8 mm longae. *Germen* cylindrico-clavatum.

Plants medium in size, to 60 cm high. *Corm* to 2 cm in diameter, covered with tunics of brown fibres and decayed remains of old leaves extending upward in a neck. *Prophylls* brown, irregularly broken and somewhat fibrous. *Leaf* canaliculate, linear, to 40 cm long, apex usually dry and decayed. *Bract leaves* 3–4, sheathing, green with dry brown apex, 4–6 cm long. *Scape* erect, usually bearing 1–2 branches. *Inflorescence* several flowered, spathe bracts green with brown apex, inner spathe 5–7 cm long, outer somewhat shorter. *Flowers* white to cream, darkly spotted at base of limbs of outer segments; *outer perianth segments* 3–3.5 cm long, limb 1.5–2 cm long and about 1.5 cm wide, claw speckled darkly, glabrous; *inner perianth segments* reduced to minute, entire or slightly 3 lobed, 5–7 mm long, acute. *Filaments* about 7 mm long, free only at apex; *anthers* 5–6 mm, white, not reaching stigmas. *Style* white, about 7 mm long, branches to 7 mm, crests slender, to 8 mm. *Ovary* cylindrical to clavate.

Flowering time: January to March.

Distribution: Southern Drakensberg from Giant's Castle to Engcobo (Fig. 9).

Although this species has been known to science since the 1890's when it was found by H. Bolus in East Griqualand, it has remained undescribed. It is quite unlike any other species of *Moraea*, although perhaps is most closely related to *M. pubiflora*. The reduced size of the inner perianth segments with their almost

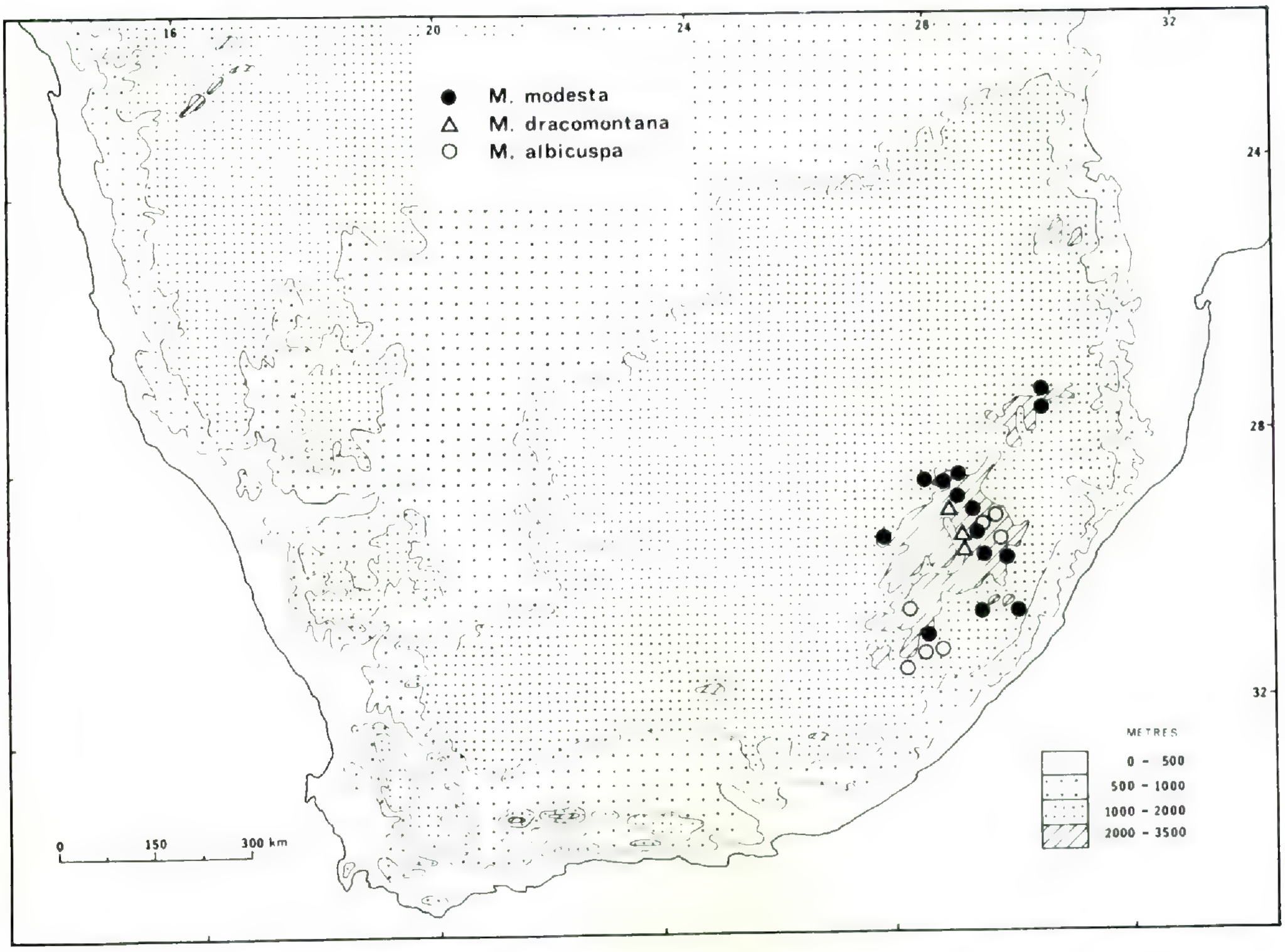

FIGURE 9. Distribution of *Moraea albicuspa*, *M. dracomontana*, and *M. modesta*.

or entirely absent lobing makes it easily recognisable and it is unlikely that it could be confused with any other species.

29.29 (Underberg): Bannerman Pass (-AB), *Trauseld 556* (NU, PRE); Giants Castle Game Reserve (-AD), *Trauseld 955* (PRE); top of Sani Pass (-CB), *Ruch 2443* (PRE, ROML).

30.28 (Matatiele): Drakensberg summit, Tina River (-AC), *Galpin 6846* (BOL, PRE, SAM).

31.28 (Umtata): Near Maclear (-AB), *H. Bolus 10307* (BOL); Ntywenka (-BA), *Hilliard & Burtt 3747* (NU); Engcobo mountain (-CA) *H. Bolus 10306* (BOL).

11. **Moraea dracomontana** Goldbl., sp. nov. Type: Langabalela Pass, Giant's Castle, *Trauseld 500* (PRE, holotype, CPF, NU, isotypes).

Planta ad 30 cm alta. *Cormus* ad 1 cm diam., munitus tunicis pallidis brunneis fibrosis. *Prophylla* membranacea, scapum vaginantia, saepe fracta et fibrosa. *Folium* teres an subteres, saepe siccum ad apicem. *Scapus* gracilis, erectus, raro ramosus. *Folia vaginantia* 2, ad 5 cm longa, virides, apicibus brunneis. *Inflorescentia* pauciflora, spatha interiora ad 5 cm longa, exteriore minori prope dimidio. *Flores* malvino-purpurei, luteo notata; *perianthii segmenta exteriora* 2.5–3 cm longa, limbus ad 1.8 cm longus; *segmenta interiora* 5–10 mm longa, trifida, cuspo medio acuto, longiore an breviore quam lateralibus, lobis lateralibus linearibus, apicis expansis, obtusis. *Filamenta* ad 6 mm longa, connata ad dimidium longitudinis; *antherae* 6 mm longae, malvinae. *Stylus* connatus sole ad basem, rami ad 8 mm longi, cristae lanceolatae, ad 6 mm longae. *Germen* cylindrico-clavatum.

Plants small, reaching to 30 cm high. *Corm* about 1 cm in diameter covered with tunics of fine light brown fibres and decayed leaves and prophylls extending upwards in a neck. *Prophylls* brown, irregularly broken, extending well above ground. *Leaf* sub-terete, with adaxial groove, about as long as stem, often broken

above. *Bract leaves* 2, entirely sheathing, 3–4.5 cm long, green with brown apex. *Scape* erect, rarely branched. *Inflorescence* several-flowered, spathe bracts green, with dry, brown apex, inner spathe about 5 cm long, outer a little more than half this length. *Flowers* mauve-purple with a yellow nectar guide; *outer perianth segments* 2.5–3 cm long, limb to 1.8 cm long; *inner segments* 5–10 mm long, trifid, outer lobes linear with expanded apex, obtuse, inner cusp slender, acute, either shorter or longer than the lateral lobes. *Filaments* to 6 mm, joined in lower half; *anthers* 6 mm long, mauve, not reaching the stigmas. *Style* joined at base only, branches about 8 mm long, crests lanceolate, to 6 mm long. *Ovary* cylindrical-clavate.

Flowering time: December to January.
Distribution: Drankensberg, high altitudes (Fig. 9).

Moraea dracomontana is known from only three collections, and it is clear that this species is far from being satisfactorily understood. Although all too little is known of its distribution or variation, it has the appearance of a distinct species. It is allied to *M. pubiflora* and *M. modesta* but seems intermediate between the two. The characteristic three-lobed inner perianth segments and the purple color of the flowers make *M. dracomontana* easy to distinguish.

28.28 (Bethlehem): Ox Bow camp (-DB), *Jacot-Guillarmod 4154* (PRE).
29.29 (Underberg): Langabalela Pass (-AD), *Trauseld 500* (CPF, NU, PRE); Sani Pass (-CB), *Hilliard 950* (NU).

12. **Moraea modesta** Killick, Bothalia 6: 437. 1954. Type: Cathedral Peak Forest Station, *Killick 1028* (PRE, holotype).

Plants small, 10–20 cm high, rarely more. *Corm* to 1 cm diameter covered with tunics of very fine fibres and old leaf bases which extend upwards in a neck. *Prophyll* membranous, sheathing base of stem, often broken and fibrous. *Leaf* terete, with adaxial groove; the leaf attached to flowering stem often dead and dry, sometimes absent, and a new leaf may be present but not fully developed at time of flowering. *Stem* slender, erect, rarely branched. *Bract leaves* 2 or rarely 3, to 5 cm long, sheathing, green, with dry, brown apex. *Inflorescence* few-flowered, spathes green, inner 3–5 cm long, outer two-thirds as long. *Flower* white to pale mauve, veined with purple; *outer perianth segments* 2–2.7 cm long, limb to 1.5 cm long and 1.5 cm wide; *inner segments* minute, to 6 mm long, linear or trifid with inner cusp longest, about 1 mm. *Filaments* to 6 mm long, free near apex only, anthers about 6 mm long. *Style* to 4 mm long, branches about 7 mm long, narrow, crests linear, about 6 mm long. *Ovary* cylindrico-clavate, to 8 mm long.

Flowering time: Spring to early summer.
Distribution: Drakensberg from Kokstad to Wakkerstroom, 1,800–3,000 m (Fig. 9).

Icones: Killick, Bothalia 6: 438. 1954; Trauseld, Wild Flowers of the Natal Drakensberg. 35, *fig. 299*. 1969.

This small plant was first described by Dr. D. J. B. Killick in 1954, who reported that it occurred on grass slopes in the Drakensberg at altitudes of between

2,000 and 3,000 m. More material, since examined, confirms this observation in general, although it is now known to occur over a wider range, from Kokstad in the south to Wakkerstroom in the north and including the whole of Lesotho. It has also been recorded from somewhat lower altitudes of about 1,800 m.

Moraea modesta is a small member of the group *Vieusseuxia*, and it is quite distinct from other members of this group. Its closest ally is perhaps *M. dracomontana*, but the terete leaf, often dead at flowering time, and the small, pale colored flower are good distinguishing characters which make it unlikely that *M. modesta* would be confused with other species.

27.30 (Vryheid): Oshoek, Wakkerstroom district (-AC), *Devenish 104, 1370* (PRE); Donkerhoek, Utrecht district (-AD), *Devenish 697* (PRE).

28.28 (Bethlehem): Leribe district (-C), *Dieterlen 813* (PRE); Golden Gate Park (-DA), *Liebenberg 7327* (PRE); Mont aux Sources (-DB), *Galpin 10372* (PRE); summit of Mont aux Sources (-DD), *Flanagan 2041* (BOL).

28.29 (Harrismith): Cathedral Peak area (-CC), *Killick 1028* (PRE); near Castle Butress, *Killick 1854* (BOL); Cathedral Peak Forest Station (-CD), *Killick 1551 A & B* (PRE).

29.27 (Maseru): Thaba Bosiu district (-BC), *Dieterlen 1064* (PRE).

29.29 (Underberg): Giants Castle Game Reserve (-AD), *Trauseld 406* (CPF, NU, PRE); *Trauseld 299* (CPF, NU); *Edwards 2168* (NU); *Skead 212* (CPF, NU); Giants Castle, *Wylie s. n.* (NH 10566); Umgeni Poort (-BD), *Moll & Mauve 2240* (PRE); Impendhle (-DB), *Levett 55* (NH).

30.28 (Matatiele): 25 km S of Mount Fletcher (-CD), *Killick & Marais 2075* (PRE).

30.29 (Kokstad): Mount Currie (-AD), *McLoughlin s. n.* (PRE 26266).

30.30 (Port Shepstone): Highflats, Polela district (-AC), *Lansdell s. n.* (NH 37539).

13. **Moraea trifida** Foster, Contr. Gray Herb. 114: 49. 1936. Type: As for *M. rogersii* N. E. Br.—Fig. 3C.

Moraea rogersii N. E. Br., Trans. Roy. Soc. S. Africa 17: 348. 1929, *non* Baker (1892). Type: Pilgrims Rest, *Rogers s. n.* (K, holotype).

Moraea culmea Killick, Bothalia 6: 436. 1954. Type: Cathedral Peak, *Killick 1558* (PRE, holotype, BOL, K, LD, NBG, NU, P, isotypes).

Plants small to medium, sometimes to 55 cm high. *Corm* 1–2 cm in diameter, with tunics of straw-colored fibres. *Prophylls* pale brown, reaching shortly above the ground. *Leaf* produced from stem some distance above ground; varying in degree of development when flowering; canaliculate, to 4 mm wide, to 60 cm long. *Bract leaves* 1 or 2 (–3), herbaceous with brown dry apex, 5–6 cm long. *Scape* erect, simple or several branched, branches erect. *Inflorescence* several flowered, spathes green, brown tipped, 3.5–7 cm long, outer spathe 1–2 cm shorter. *Flowers* yellow to cream, dotted brown to green; *outer perianth segments* spreading, reflexed at knee, lanceolate, 1.5–2 cm long, limb 0.8–1.0 cm long and 5–10 mm wide; *inner segments* to 1.5 cm high, erect, trifid; outer lobes short, ovoid, inner a long slender erect cusp to 7 mm long. *Filaments* to 9 mm long, free for last 1.5 mm, *anthers* to 4 mm long, often extending beyond the stigma in old flowers. *Style* to 7 mm long, branches about 4 mm long, crests slender to 4 mm long. *Ovary* clavate, 7–0 mm long; *capsule* barrel-shaped, to 2 cm long, about 0.5 cm wide.

Flowering time: Late spring to autumn—November to March, rarely later.

Distribution: Grassland from eastern Cape to south eastern Transvaal (Fig. 10).

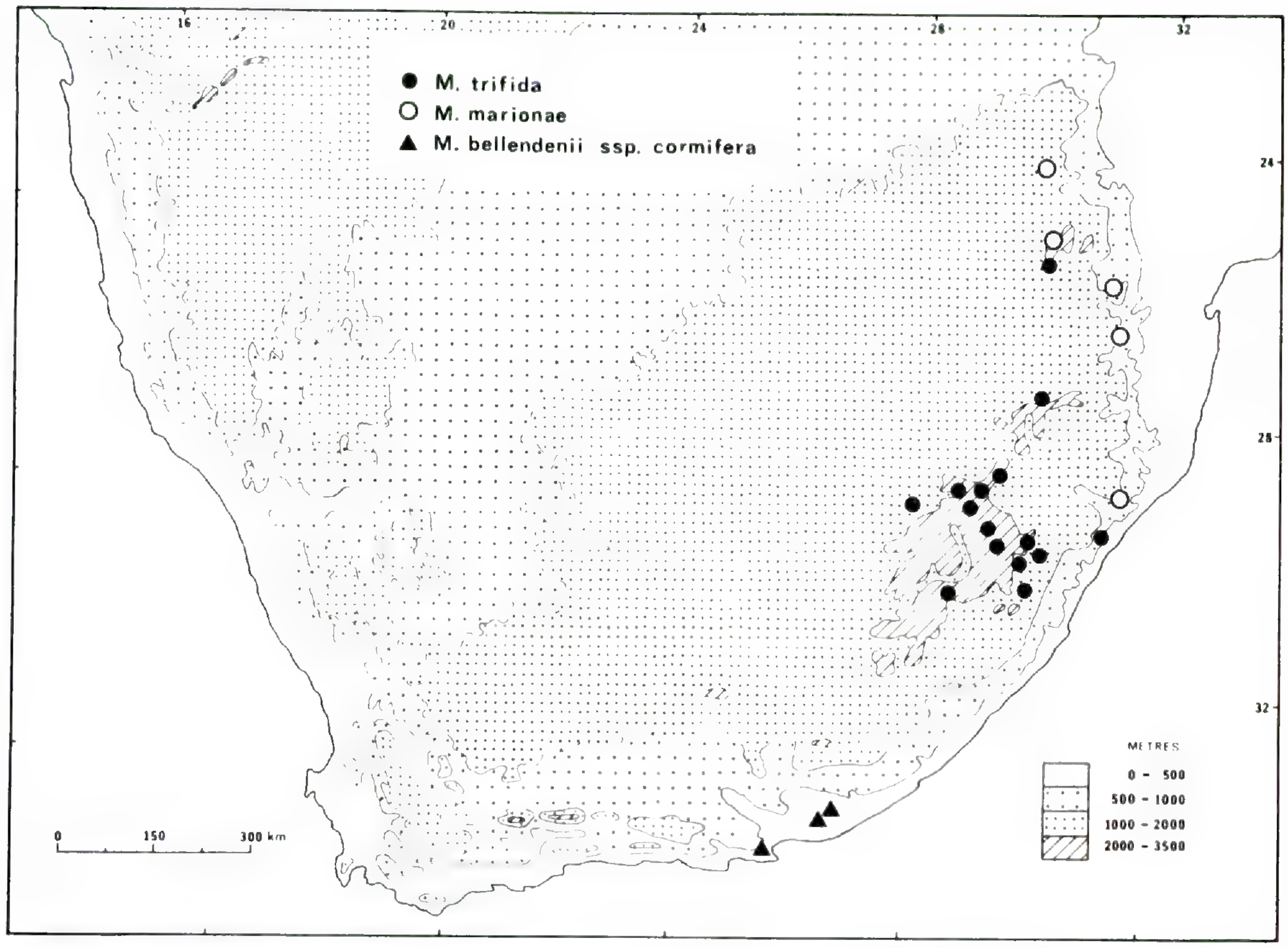

FIGURE 10. Distribution of *Moraea trifida*, *M. marionae*, and *M. bellendenii* subsp. *cormifera*.

Icones: Killick, Bothalia 6: 436. 1954; Trauseld, Wild Flowers of the Natal Drakensberg. 35, *fig. 474.* 1969.

This species was first described by N. E. Brown as *Moraea rogersii*, but this name was unfortunately a later homonym, having already been used by Baker. Foster renamed the plant, which is now known as *M. trifida*.

Moraea culmea, described by Dr. Killick, is reduced to synonymy here. An examination of the type collections of *M. culmea* and *M. trifida* (*M. rogersii*) reveals that there are very few differences and the flower structure is identical. *Moraea culmea* is smaller and has only a single bract leaf, while the taller, more robust *M. trifida* has two bract leaves. The features of size and number of bract leaves were studied in detail and found to have no significance. In general, early flowering plants are smaller, have a short leaf, and have one bract leaf, while the later flowering plants are taller, have a longer leaf, and have two or even three bract leaves. In spite of this loose correlation, some plants from the same collection may have one or two bract leaves and vary considerably in height and in length of the produced leaf.

25.30 (Lydenburg): Dullstroom (-AC), *Noome s. n.* (PRE 20797).
27.30 (Vryheid): Naauwhoek, Utrecht district (-AC), *Devenish 1256* (PRE).
28.27 (Senekal): Ficksburg (-DD), *Fawkes s. n.* (NBG 58945).
28.28 (Bethlehem): Tugela valley, Royal Natal National Park (-DA), *Hafstrom & Acocks 326* (PRE); Bestersvlei (-DB), *Flanagan 2044* (PRE); *H. Bolus 8255* (BOL).
28.29 (Harrismith): Van Reenen (-AD), *Wood 11410, 5608* (NH); Van Reenens Pass,

Marais 334 (PRE); Cathedral Peak Forest Reserve (-CA), *Killick 1558* (BOL, LD, NU, PRE, NBG), *1209* (PRE).

29.29 (Underberg): Mokhotlong district (-A), *Jacot-Guillarmod 1165* (PRE); Phutha (-AA), *Compton 21572* (NBG); Giants Castle (-AD), *Symons 445, 168* (PRE); Giants Castle Game Reserve, *Trauseld 474* (CPF, NU, PRE); Nottingham Road (-BD), *Franks s. n.* (BOL 30821, PRE 31499); Ross, Umgeni Poort, *Moll 1415* (NU); Impendhle (-DB), *Huntley 442* (PRE).

29.30 (Pietermaritzburg): Liddesdale (-CA), *Wood 4252* (NH).

29.31 (Stanger): Ensikeni (-AC), *Haygarth s. n.* (NH 12059).

30.28 (Matatiele): Quachas Nek (-BA), *Fawkes s. n.* (SAM 5425).

30.29 (Kokstad): Maxwell, Ixopo (-BB), *Evans 275* (NH).

14. **Moraea marionae** N. E. Br., Trans. Roy. Soc. S. Africa 17: 347. 1929. Type: Woodbush, *Miss Blenkison sub Moss 15565* (K, holotype).

Moraea exilis N. E. Br., Trans. Roy. Soc. S. Africa 17: 348. 1929. Type: Saddleback, Barberton, *Galpin 467* (K, holotype, PRE, isotype).

Plants small, rarely reaching 30 cm in height. *Corm* about 1 cm in diameter, covered with a tunic of pale straw-colored fibres which sometimes extend upwards in a neck. *Prophylls* short, pale, sheathing base of scape. *Leaf* solitary, absent in flowering specimens, presumably produced after flowering. *Bract leaves* usually two, lower produced very near ground, entire sheathing, herbaceous with dry brown apex, 2.4–4.5 cm long. *Scape* erect, slender, simple. *Inflorescence* several flowered, spathe bracts herbaceous with brown apex, inner to 5 cm long, outer about two-thirds as long. *Flowers* white to pale blue, marked with lilac veins; *outer perianth segments* 1.5–2 cm long, limb longer than claw, lanceolate; *inner segments* 1–1.2 cm long, erect, three lobed, outer lobes short, ovoid; inner forming a long slender cusp. *Filaments* about 5 mm long, joined for most of the length; *anthers* to 4 mm long, extending shortly above stigmas in older flowers. *Style* joined at base, branches about 4 mm long, crests slender, to 3 mm long. *Ovary* clavate; *capsule* barrel shaped, to 1 cm long.

Flowering time: August to October.

Distribution: Grassland, Zululand to Haenertsburg (Fig. 10).

As treated here, *Moraea marionae* and *M. exilis*, both described by N. E. Brown in 1929, are regarded as conspecific. No differences of any significance can be detected between the two, although *M. marionae* was recorded from Haenertsburg, while *M. exilis* was found at Barberton. It was decided to recognise *M. marionae* and reduce *M. exilis* to synonymy, because the description of the former species was more detailed and the type material is in better condition and is thus less liable to cause confusion. The type collection is in the Kew Herbarium and consists of 5 short flowering stems, one with a corm. A second collection apparently collected by Moss is fruiting material from the type locality and specimens of this later collection are to be found both at Kew and at the National Herbarium, Pretoria. *Moraea marionae* is undoubtedly closely allied to *M. trifida*, both species having the same floral structure, and they differ mainly in the presence or absence of a leaf at flowering time. Further study and if possible, cultivation, are needed to determine whether the two species are in fact distinct. It is unfortunate that *M. marionae* is poorly collected, but it is obviously a small, inconspicuous plant and thus could easily be overlooked.

One point not yet known about it is the nature of the leaf. All specimens collected lack a leaf at the flowering time, and it is not known whether this is a consistent feature, similar to that found in *M. stricta*. It is possible that *M. marionae* is simply a very early flowering form of *M. trifida*, but small differences in size and flower color support the contention that *M. marionae* is distinct.

23.29 (Pietersburg): Woodbush mountains (-DD), *Moss 15565* (PRE).
25.30 (Lydenburg): Steenkampsberg (-AA), *Codd 9833* (PRE); Mount Anderson (-BA), *Humbert 10957* (P).
25.31 (Komatipoort): Saddleback Ridge (-CC), *Galpin 467* (PRE).
28.31 (Nkandla): Eshowe (-CD), *Lawn 999* (NH); *Galpin 13539* (PRE).
Unknown locality: Swaziland, *Stewart s. n.* (PRE 10563).

15. **Moraea bellendenii** subsp. **cormifera** Goldbl., subsp. nov. Type: Atherstone area, Albany district, *Jacot-Guillarmod 6706* (RUH, holotype, GRA, isotype).

Planta ad 40 cm alta. *Folium basale* canaliculatum, 5 mm latum, axilla cormifera. *Scapus* simplex an pauciramosus. *Flores* lutei aut cremei, brunneo et auro punctato: *perianthii segmenta exteriora* ad 2.5 cm longa, circa 1.5 cm lata: *segmenta interiora* trifida, lobus interior gracilis, acutus, incurvus et spiralis.

Plants comparatively small, seldom exceeding 35 cm. *Corm* to 1.4 cm in diameter with tunics of fine straw-colored fibres. *Basal leaf* linear, canaliculate, to 5 mm wide, usually bearing a large cormlet in the axil. *Stem* simple or few-branched. *Inflorescence* 3–6 cm long, spathes herbaceous with brown acuminate apices. *Flowers* yellow to cream, spotted brown to gold; *outer perianth segments* about 2.5 cm long and 1.5 cm wide, limb comparatively wide; inner segments trifid, inner lobe cusp-like, incurved or spirally coiled. *Filaments* united to base of anthers. *Style* branches about 4 mm long, crests lanceolate. *Ovary* clavate, capsule to 12 cm long and 5 mm wide. *Seeds* angled.

Flowering time: October.

Distribution: Recorded from the Grahamstown and Port Elizabeth districts (Fig. 10).

This subspecies of *Moraea bellendenii* can be distinguished by its smaller size, fewer branches and the unusual character of the large cormlet in the axil of the basal leaf. Subspecies *cormifera* does not appear to be common and is not well known in its habitat. Typical *Moraea bellendenii* is a common late spring-flowering species in the western Cape, but it has been recorded as far east as Knysna and Humansdorp. Forms at the eastern extremity of the range are quite typical, robust, tall plants (45–100 cm), with many branches and do not have a large axillary cormlet characteristic of subsp. *cormifera*. The new subspecies, known from Port Elizabeth and east to Grahamstown, is not isolated from the typical subspecies by any great distance, and later collections in the intervening area may yield intermediates, but in their absence, it seems advisable to consider the eastern Cape form of *M. bellendenii* a distinct subspecies.

33.25 (Port Elizabeth): Baakens River valley (-DC), *F. Cruden 399* (GRA).
33.26 (Grahamstown): Atherstone area (-BC), *Jacot-Guillarmod 6706* (GRA, RUH); Grahamstown brickfields, *Misses Daly and Cherry 41* (GRA); *Dyer 1661* (GRA).

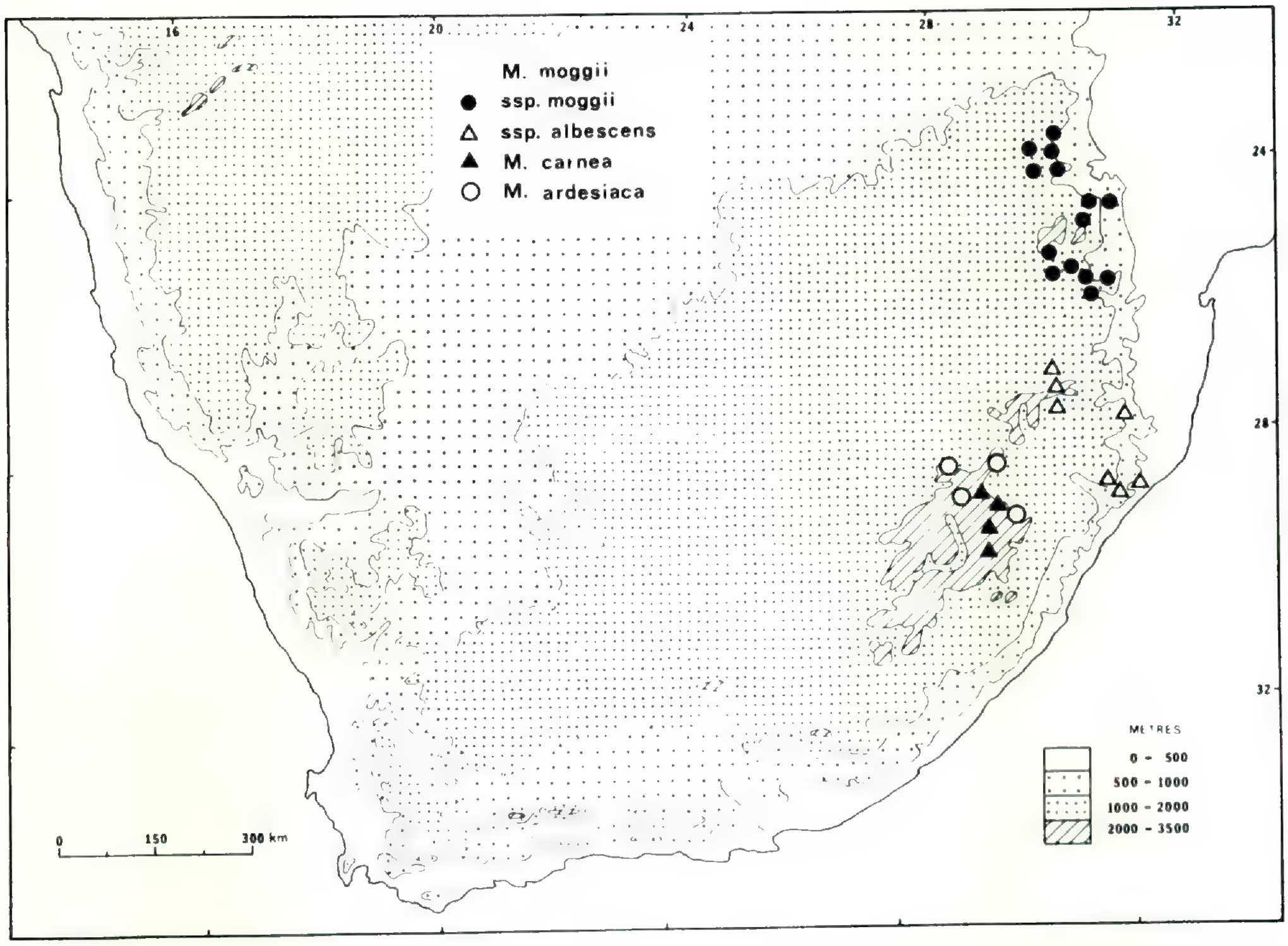

FIGURE 11. Distribution of *Moraea moggii* subsp. *moggii* and subsp. *albescens*, *M. carnea*, and *M. ardesiaca*.

Group V: GRANDIFLORA

16. **Moraea moggii** N. E. Br., Trans. Roy. Soc. S. Africa 17: 346. 1929. Type: Struben's farm, *Mogg s. n.* (PRE 15652, holotype).

Plants medium to tall, usually slender, to 70 cm high, always solitary. *Corm* to 2 cm in diameter, frequently covered by matted fibres of previous season's decayed leaf bases. *Prophylls* brown, purplish below, firm, entire or irregularly broken, not forming a fibrous network above. *Basal leaf* linear, canaliculate, exceeding inflorescence, to 1.5 cm wide. *Scape* erect, simple. *Bract leaves* (2–)3(–4), herbaceous, with dry brown apex, generally not overlapping. *Inflorescence* several flowered, 9–16 cm long, inner spathe slightly shorter. *Flowers* yellow, cream or white, with bright yellow nectar guide, and purple veined; *outer perianth segments*, broadly lanceolate, obtuse, 4–7.5 cm long, limb to 5 cm long and to 3.5 cm wide; *inner perianth segments* erect, broadly lanceolate with tapering base, obtuse to retuse, to 6 cm long and 2–2.5 cm wide. *Filaments* about 1 cm long, joined for about half their length; anthers about 1 cm long, not reaching the stigma. *Style* about 8 mm long, branches to 2 cm long, crests 1–2 cm long. *Ovary* linear 2–3 cm long; *capsule* to 4 cm long; *seeds* depressed, disciform. *Chromosome number* (subsp. *moggii*) $2n = 12$, *Goldblatt 86* (J).

Flowering time: December to May.

Distribution: Grassland, from Haenertsburg, northern Transvaal to northern Natal and Zululand (Fig. 11).

Icones: Sealy, Bot. Mag., n. s. *Tab. 469.* 1965; Letty, Wild Flowers of the Transvaal. *Pl. 36, fig. 2.* 1962. (Both are subsp. *moggii.*)

Moraea moggii can be distinguished from other members of the *Grandiflora* group by its solitary habit, slender, canaliculate leaf, and large flower. It is most easily confused with *M. spathulata*, some forms of which are very similar, but the two can usually be distinguished by the solitary habit of *M. moggii* compared with *M. spathulata*, which typically grows in clumps. Apart from this, *M. moggii* is generally a late flowering species, while *M. spathulata* flowers in spring or summer, excepting *M. spathulata* subsp. *autumnalis* which occurs in southern Natal and the adjoining area of the Cape Province.

Some doubt has been thrown on the identity of the type of *M. moggii*, a specimen collected by Dr. A. O. D. Mogg and housed at the National Herbarium. The locality given on the label is Struben's Farm, Pretoria, an area where *M. moggii* does not grow. When asked about the problem, Dr. Mogg suggested that the plant originally came from Haenertsburg, where his family once farmed. Although he was not positive on this point, his suggestion does seem likely, for the plant typified by *M. moggii* is very common around Haenertsburg. A photograph accompanying the type specimen also adds confusion, as this is of a small flowered plant, not *M. moggii*, but probably *M. stricta*. There is, however, no reason to reject *M. moggii*, because N. E. Brown indicated quite clearly the type specimen, and this can readily be matched with plants occurring in the Haenertsburg area.

Moraea moggii has been divided into two subspecies, occurring in different parts of the summer rainfall area. These have in common the solitary habit, and slender canaliculate leaf, combined with fairly large size, and all forms grow in open, short grassland, usually in montane areas. *Moraea moggii* may be found later to be an unnatural species, but it is difficult if even possible to satisfactorily distinguish the various forms, races, and the two subspecies on any but geographical grounds.

KEY TO THE SUBSPECIES

1. Flowering in late February to April; flowers yellow; occurring in the eastern Transvaal and Swaziland ..... a. subsp. *moggii*
1'. Flowering in December or January, occasionally later; flowers usually white, sometimes yellow; occurring in Zululand and the Wakkerstroom area of the Transvaal ..... b. subsp. *albescens*

16a. subsp. **moggii**

Prophylls firm, dark brown above, paler and veined below, inner rarely less than 15 cm long. *Leaf* grey-green, glaucous, 4–10 mm wide, not ribbed when fresh. *Flowers* yellow, veined purple-brown.

Flowering time: Late February to April.

Distribution: Short grassveld, from Haenertsburg to Mbabane, on mountain slopes (Fig. 11).

The typical subspecies can be distinguished from the other subspecies by its glaucous leaf, well-developed prophylls, and otherwise by its distribution in the

eastern Transvaal and Swaziland. It is typically autumn flowering but has been found in flower as early as February and as late as May.

23.29 (Pietersburg): Wolkberg (-DD), *Meeuse 9910* (PRE).
23.30 (Tzaneen): Sarahsdrift (-CA), *Scheepers 622* (PRE); Duiwelskloof, *Scheepers s. n.* (PRE); Magoebas Kloof Hotel (-CC), *Mauve 4787* (PRE).
24.29 (Zebediela): Ashmole Dales (-BB), *Pole-Evans s. n.* (PRE 19012).
24.30 (Pilgrims Rest): The Downs (-AA), *Junod 4135* (PRE); *Codd & Dyer 7750* (PRE); Three Sisters Mountain (-DB), *Galpin s. n.* (BOL 30819); Belvedere, Graskop district (-DD), *Davidson 165* (J).
24.31 (Acornhoek): Klaserie (-CA), *Holland s. n.* (BOL 30820).
25.30 (Lydenburg): Santa siding (-AC), *Reynolds 2309* (PRE); between Lunsklip and Belfast (-CA), *Mauve & Leistner 3273* (PRE); Waterval Boven (-CB), *Rogers 14469* (PRE); Mashonamini, Airlie (-DA), *Cross 109* (NBG); Nelsberg, Barberton (-DD), *Reynolds 2277* (PRE).
25.31 (Komatipoort): Barberton (-CC), *van Dam s. n.* (PRE 21157).

16b. subsp. **albescens** Goldbl., subsp. nov. Type: Tafelkop near Wakkerstroom, *Mauve & Tolken 4524* (PRE, holotype, BOL, isotype).

Prophylla rigida ad submembranacea, brunnea, interius raro excedentum 15 cm, plerumque circa 10 cm longum. *Folium* ad 1.5 cm latum, pallidum, viridis aut aliquantum glaucum, nervis prominentibus etiam in vivo. *Flores* albi, cremei aut lutei, viridibus aut purpureo-brunneis nervosis. *Rami styli* et cristae saepe purpurascentes.

Prophylls firm to submembranous, light brown, inner seldom reaching more than 15 cm in length, usually less than 10 cm. *Leaf* to 1.5 cm wide, light green or somewhat glaucous, veins occasionally prominent even in fresh material. *Flowers* white, cream or sometimes yellow, veined green, purple or brown; *style branches* and crests often suffused with purple.

Flowering time: Summer, occasionally extending to late autumn.

Distribution: Open grassland in Zululand and eastwards to the Utrecht–Wakkerstroom area (Fig. 11).

Moraea moggii subsp. *albescens* appears at first to be a very distinct taxon, but when the whole range of material from areas surrounding the type locality are examined, plants are found to differ in color and time of flowering, and it becomes increasingly difficult to distinguish it from subsp. *moggii*. Indeed it is possible that subspecific rank is too high, but in the absence of intermediates in the intervening areas of southern Swaziland, this taxon should be accorded recognition at subspecific level.

27.30 (Vryheid): Tafelkop, Wakkerstroom (-A), *Mauve & Tolken 4524* (PRE); near Wakkerstroom (-AC), *Devenish s. n.* (PRE); Donkerhoek, Utrecht district, *Devenish 544, 1253* (PRE); Wakkerstroom, *van Dam s. n.* (PRE 24322).
27.31 (Louwsberg): Ngome (-CD), *Strey 9426* (PRE).
28.31 (Nkandla): 18 km W of Melmoth (-CA), *Schelpe 5181* (BOL, SAM); Melmoth (-CD), *Gerstner 4315* (PRE); near Entumeni, *Wood 3960* (NH, SAM); near Eshowe, Umhlatuzi valley (-D), *Gerstner s. n.* (NH 22560).
Unknown localities: Lancaster Hill summit, *Galpin 9759* (PRE); Zululand, *Wylie s. n.* (NH 2446).

17. **Moraea muddii** N. E. Br., Trans. Roy. Soc. S. Africa 27: 346. 1929. Type: Mac Mac Creek, *Mudd s. n.* (K, holotype).—Fig. 2A.

Plants 15–70 cm but usually about 35 cm high, solitary. *Corm* about 1.5 cm in diameter, sometimes covered by straw-colored fibres of previous seasons.

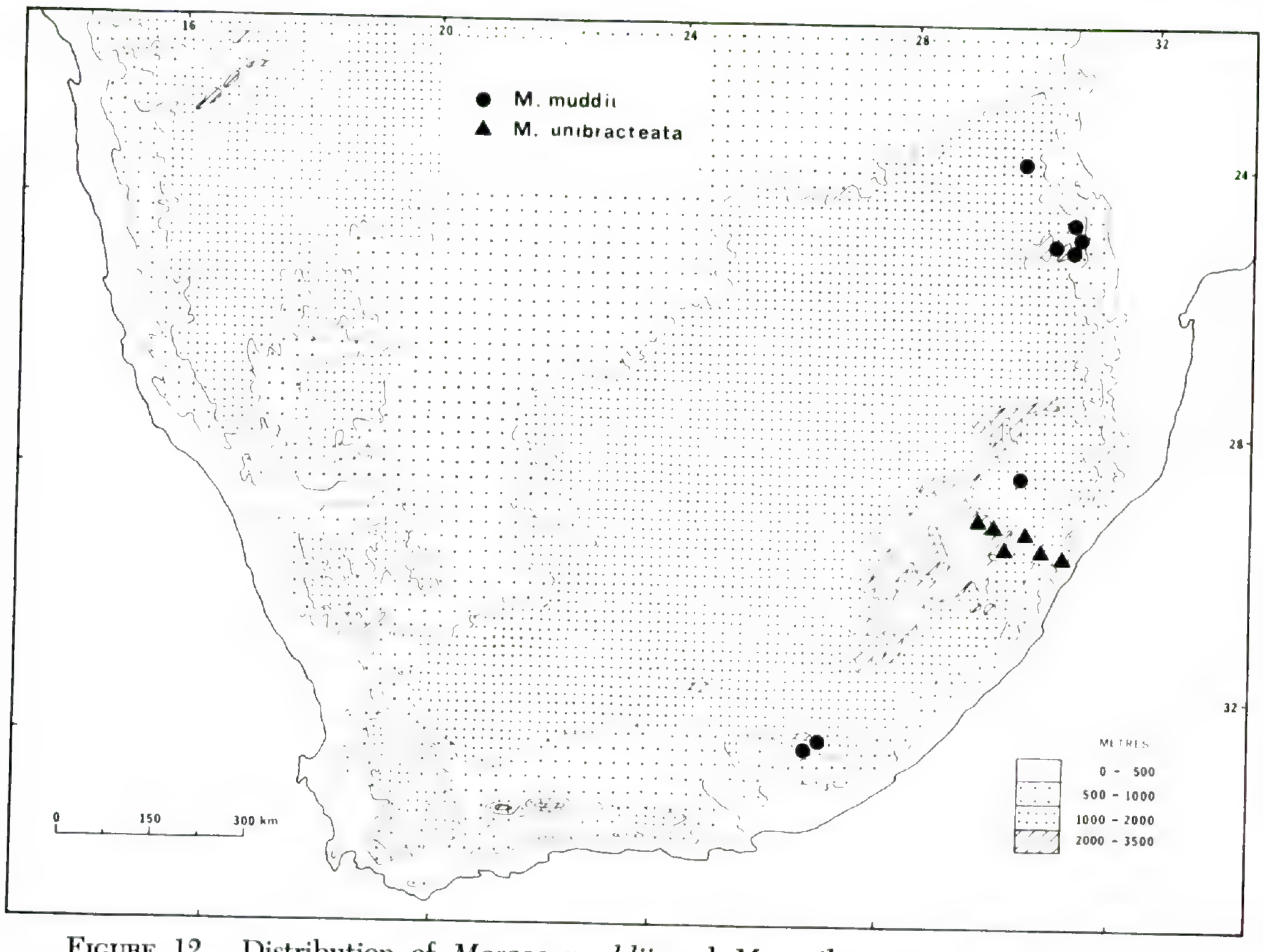

FIGURE 12. Distribution of *Moraea muddii* and *M. unibracteata*.

Prophylls brown, usually broken vertically into irregular strips. *Leaf* linear, canaliculate, rarely to 6 mm wide, usually overtopping the inflorescence. *Scape* erect, unbranched, covered by two bract leaves. *Bract leaves* 2–3, entirely sheathing, herbaceous with dry apex, 8–12 cm long. *Inflorescence* several flowered, 7–12 cm long, usually about 9 cm; outer spathe somewhat shorter than inner; apices dry, brown. *Flowers* yellow; *outer perianth segments* lanceolate, 3.5–5 cm long, 1.2–2 cm wide, claw 1.5–2 cm long; *inner segments* lanceolate, to 3.5 cm long and 7 mm wide. *Filaments* up to about 1 cm long, joined for lower two-thirds; *anthers* to 9 mm long, not reaching the stigma. *Style* about 3 mm, branches to 1.3 cm, crests about 1 cm long. *Ovary* oblong, about 1.5 cm long. *Seeds* disc shaped, testa spongy.

Flowering time: October to December, rarely later.

Distribution: Mountainous regions of the summer rainfall area (Fig. 12).

Moraea muddii, one of the smallest of the yellow flowered species of *Moraea*, occurs in rather moist grassland along the mountain ranges of the summer rainfall area. It flowers from late spring to midsummer and rarely later, although it has been found in bloom during March.

Its distinguishing characters are mostly quantitative, the plant and its flowers generally being comparatively small, although considerable variation does exist. The nature of the prophylls, being soft, brown, and irregularly broken vertically is also characteristic (Fig. 2A). Its small size and solitary habit distinguish it from *Moraea spathulata*; its very slender leaf, comparatively soft prophylls, and early

flowering period from the forms of *M. moggii*; and its several bract leaves from *M. unibracteata*. This last mentioned species is probably very closely allied to *M. muddii* and may be found to be a regional race occurring in Natal. Further collections are necessary to clarify this point. *Moraea muddii* has a rather disjunct range, being common in the mountains of the eastern Transvaal and occurring again in the eastern Cape, where only a few collections have been made, some as far west as the Hogsback. This break in the distribution pattern is unusual, but the plants from both areas are similar and do not appear to be different to any significant degree. There also seems little doubt that *M. muddii* does not occur in the Natal Drakensberg, where it would be expected, for this area has been well collected.

23.29 (Pietersburg): Haenertsburg (-DD), *Eastwood s. n.* (PRE 14894).
24.30 (Pilgrim's Rest): Graskop (-DD), *Louw 2391* (PRE); *Galpin 14529* (PRE); *Thorncroft 988* (PRE); God's Window, *Mogg & Davidson 32989* (J).
25.30 (Lydenburg): Mount Anderson, (-BA), *Galpin 13585* (BOL, PRE); Sabie/Lydenburg road, *Codd 4420* (PRE); Sabie Falls (-BB), *Burtt-Davy 1548* (BOL); Sabie Valley (-BB), *Grant s. n.* (K).
28.30 (Dundee): Kafir Drift, Utrecht (-CA), *Thode 362A* (NH, PRE).
32.26 (Fort Beaufort): Hogsback Mountain (-DB), *Rattray 400* (BOL); Gaika's Kop, Amatolas, *Grant 3068* (BOL, MO).

18. **Moraea unibracteata** Goldbl., sp. nov. Type: Nottingham Road, *Galpin 9457* (PRE, holotype, CPF, NU, isotypes).

Planta ad 35 cm alta, solitaria. *Cormus* circa 1 cm diam., munitus paucis tenuibus fibris. *Prophylla* brunnea integra aut fracta irregulariter. *Folium basale* inflorescentiam excedens, 0.2–1 cm latum, canaliculatum. *Ccapus* erectus simplex. *Folium vaginans* solitarium, prope basem inflorescentiae insertum, inflorescentiam imbricatum. *Inflorescentia* pauciflora, spathae 6–8 cm longae, exterior aliquantum brevior. *Flores* pallidi lutei, purpureis venis (flores sicci raro caerulei); *perianthii segmenta exteriora* 3–4.5 cm longa, lanceolata; *segmenta interiora* 3–4 cm longa. *Filamenta* ad 8 mm connata in pars inferiore; *anthera* 7–9 mm. *Stylus* 4–5 mm longus, rami ad 1 cm longi, crista ad 1–3 cm longa. *Germen* ad 1.8 cm longum.

Plants small, to 35 cm high, solitary. *Corm* about 1 cm in diameter, covered by fine, pale fibrous tunics. *Prophylls* pale brown, entire or more usually broken irregularly. *Basal leaf* exceeding the inflorescence, 0.2–1 cm wide, canaliculate. *Scape* erect, simple. *Bract leaf* solitary, inserted at base of inflorescence and overlapping the spathes. *Inflorescence* few-flowered, spathes 6–8 cm long, outer somewhat shorter. *Flowers* pale yellow, veined with purple (drying pale blue occasionally); *outer perianth segments* 3–4.5 cm long, lanceolate; *inner segments* 3–4 cm long, narrowly lanceolate. *Filaments* about 8 mm long, joined in lower part; *anthers* 7–9 mm long. *Style* 4–5 mm long, branches about 1 cm long, crests to 1.3 cm long. *Ovary* to 1.8 cm long.

Flowering time: October to November.
Distribution: Natal Midlands and the lower altitudes of the Drakensberg (Fig. 12).

All too little is known about *Moraea unibracteata*, which appears somewhat intermediate between *M. muddii* and *M. spathulata*. From the observations recorded on the few specimens collected, *M. unibracteata* is clearly a representative of the *Grandiflora* group, and its small size and similar prophylls indicate a close relationship to *M. muddii*. It can, however, always be recognised by having only

a single bract leaf, located just below the inflorescence, and overlapping the spathes.

29.29 (Underberg): Giants Castle, Meander Valley (-AB), *Trauseld 450* (NU, PRE), *1011* (PRE); Mooi River district (-B), *Mogg 3142* (PRE); Tabamhlope (-BA), *Wylie s. n.* (NU 41862); Impendhle (-DB), *Levett 51* (NH).

29.30 (Pietermaritzburg): Curry's Post (-AC), *Mogg 6445* (PRE); Nottingham Road, *Galpin 9457* (PRE); Inanda (-DB), *Wood 487* (SAM).

19. **Moraea carnea** Goldbl., sp. nov. Type: Giant's Castle, *Trauseld 481* (PRE, holotype, CPF, NU, isotype).

Planta ad 50 cm alta, solitaria. *Cormus* ad 1.5 cm diam., munitus fibris tenuibus reticulatis. *Prophylla* brunnea, fracta irregulariter. *Folium basale* lineare, canaliculatum, inflorescentiam excendens, ad 6 mm latum. *Scapus* erectus, simplex. *Folia vaginantia* 3–4, 4–8 cm longa, apicibus acuminatis et siccis. *Inflorescentia* pluriflora, spatha interior 7–10 cm, exterior 2–3 cm brevior. *Flores* cremei ad carnei, nervis roseis; *perianthii segmenta exteriora* ad 6 cm longa, limbus 3–3.5 cm longus et ad 2.5 cm latus; *segmenta interiora* ad 5 cm longa et ad 1 cm lata. *Filamenta* 1–1.2 cm longa, *antherae* circa 1 cm longae, breviores quam filamenta. *Stylus* 1 cm longus, rami ad 1.7 cm, cristae ad 1.5 cm longae. *Germen* circa 2 cm longum, *capsula* rostrata.

Plants medium in size, up to 50 cm high, solitary. *Corm* to 1.5 cm in diameter, covered by a fine reticulation. *Prophylls* brown, broken vertically in an irregular manner. *Basal leaf* linear, overtopping the inflorescence, to 6 mm wide, canaliculate. *Scape* erect, unbranched. *Bract* leaves 3–4, entirely sheathing, 4–8 cm long, with dry acuminate apex. *Inflorescence* several flowered, inner spathe 7–10 cm long; outer 2–3 cm shorter. *Flower* yellow-cream to flesh-colored marked with pink to brown veins, style crests uniformly brown, nectar guide yellow; *outer perianth segments* to 6 cm long, limb 3–3.5 cm long and to 2.5 cm (2–2.5) wide; *inner segments* to 5 cm long and about 1 cm broad. *Filaments* 1–1.2 cm long, joined for about two-thirds length; *anthers* about 1 cm long, shorter than the filaments, not reaching the stigmas. *Style* about 1 cm long and branches to 1.7 cm long, crests to 1.5 cm long. *Ovary* about 2 cm long; *capsule* beaked.

Flowering time: Early Summer.

Distribution: Grass slopes in the Drakensberg above 2,000 m (Fig. 11).

Icon: Trauseld, Wild Flowers of the Natal Drakensberg. 37, *fig. 418.* 1969.

Moraea carnea and the following species, *M. ardesiaca*, are closely related species, both allied to *M. muddii* and may, in fact, replace this species in the Natal Drakensberg. *Moraea carnea* and *M. ardesiaca* are the only known members of the *Grandiflora* group in South Africa that are not colored yellow to white. The color difference in a group where yellow so predominates is one of the prime reasons for recognising these as distinct species, although, of course, there are other characters of importance.

The color is by far the easiest method of recognising the two, but unfortunately in old material, without color notes, or with poorly pressed flowers, this is of little use and then less obvious features such as the prophylls must be relied upon. In the absence of the latter, and without well preserved flowers, identification is very difficult.

Moraea carnea itself has cream colored petals, veined and flushed purple to flesh pink. In most individuals the inner petals and especially the style crests

are dark pink. The key character, whether the anthers are longer (in *M. ardesiaca*) or shorter (in *M. carnea*) than the filaments, appears to be very useful and worked in all specimens examined by the author. Apart from the floral characters, it is mainly the stouter stems and firmer leaf that distinguish this species from *M. muddii*. A second species more easily confused is *M. ardesiaca*, usually a slate-blue to mauve flowered plant. Again, when flowers are badly preserved, identification is difficult, but *M. ardesiaca* is a taller plant, with a longer, broader leaf and distinctly broader petals, and in most cases this will be sufficient in distinguishing the two species. *Moraea carnea* and *M. ardesiaca* occur in the Natal Drakensberg but are not found together, the former occupying high altitudes from 2,000 m upwards and the latter usually below this. As can be expected, some overlap does occur, but, nevertheless, it seems that these two species occupy different ecological niches and that the differences between them are significant. Further collecting and examination in the wild state is still necessary to establish whether in fact these two species are distinct.

28.29 (Harrismith): Umlambonja Buttress (-CC), *Schelpe 995* (NU); Cathedral Peak Forest Station (-CD), *Killick 1145* (PRE).

29.29 (Underberg): Giants Castle (-AB), *Symons s. n.* (PRE 25242); Judge area, Giants Castle, *Trauseld 481* (NU, PRE); Sani Pass (-CB), *Hilliard 969* (NU).

20. **Moraea ardesiaca** Goldbl., sp. nov. Type: Royal Natal National Park, *Trauseld 84* (PRE, holotype).

Planta ad 70 cm alta, plerumque solitaria. *Cormus* ad 1.5 cm diam. *Prophylla* brunnea, ad 15 cm longa, fracta irregulariter. *Folium basale* canaliculatum, plerumque caulem excedens, 5–10(–25) mm latum. *Scapus* erectus, simplex. *Folia vaginantia* 2 raro 3, circa 10 cm longa. *Inflorescentia* pluriflora, spatha interior 9–14 cm, exterior 2–4 cm brevior. *Flores* ardesiaci, malvescenti-brunnei; *perianthii segmenta exteriora* ad 7.5 cm longa, limbus ad 5 cm longus et 2.5–3.5 cm latus; *segmenta interiora* 5–6 cm longa. *Filamenta* 8–10 mm longa; *antherae* ad 1.2 cm longae, aequales aut longiores quam filamenta. *Styli rami* ad 1.5 cm longi, cristae 1.5–2 cm longae. *Capsula* rostrata.

Plants medium to large, to 70 cm high, usually solitary. *Corm* to 1.5 cm in diameter. *Prophylls* light brown, to 15 cm long, irregularly broken vertically. *Basal leaf* canaliculate, usually exceeding the stem, 5–10 (–25) mm wide. *Scape* erect, simple. *Bract leaves* 2, rarely 3, about 10 cm long, situated on upper part of stem, lower part often naked. *Inflorescence* several-flowered, inner spathe 9–14 cm, outer 2–4 cm shorter. *Flower* slate-blue, pale mauve, purple-brown, nectar guide narrow, linear, light yellow; *outer perianth segments* to 7.5 cm, limb to 5 cm long and 2.5–3.5 cm wide; *inner perianth segments* 5–6 cm long. *Filaments* 8–10 mm long, joined in lower part; *anthers* to 1.2 cm long, as long or longer than the filaments, not reaching the stigmas. *Style* joined at base, branches to 1.5 cm, crests 1.5–2 cm long. *Capsule* beaked.

Flowering time: November to January.

Distribution: Drakensberg, 1800–2200 m (Fig. 11).

Icon: Trauseld, Wild Flowers of the Natal Drakensberg. 37, *fig.* 84. 1969.

As discussed under the previous species, *Moraea carnea*, *M. ardesiaca* appears to be most closely related to *M. muddii*, and possibly the former two species replace *M. muddii* in the Drankensberg area. *Moraea ardesiaca* can easily be

recognised from fresh material by its large slate-blue to mauve flowers. When dry and in the absence of color notes, recourse must be made to ecological data and careful measurement of the stamens and the perianth segments. Confusion with *M. carnea* is most common, but this species is generally smaller and has narrower perianth segments. It also occurs at higher altitudes (usually above 2,300 m), while *M. ardesiaca* is generally found below this, although some overlap appears to occur.

28.28 (Bethlehem): Along Mahai (-DA), *Schweidkerdt 737* (PRE); Royal Natal National Park (-DD), *Trauseld 84* (PRE); Devils Hoek, Royal Natal National Park, *Galpin 9510* (PRE); Devils Hoek Valley, *Galpin 30816* (BOL).

28.29 (Harrismith): Van Reenen (-AD), *Wood 12158* (PRE); *Wood 4526* (BOL, NH); *Franks s. n.* (NH 12158).

29.29 (Underberg): Highmoor, Little Berg (-BC), *Killick & Vahrmeier 3629* (PRE).

21. **Moraea graminicola** Oberm., Fl. Pl. Africa. *Pl. 1526.* 1969. Type: Clovelly farm near Mooi River, *Mauve 4466* (PRE, holotype, BOL, isotype).

Plants 25–60 cm at flowering time, solitary. *Corm* to 1.5 cm in diameter, covered with brown, reticulate tunics sometimes extending upwards a short distance. *Prophylls* 3–4, innermost rarely more than 10 cm, pale, submembranous, entire or frayed or broken at apex. *Basal leaf* usually exceeding stem at flowering time, linear, 0.7–2.5 cm wide. *Scape* erect simple (rarely branched in subsp. *notata*). *Bract leaves* 1–2 or 3, herbaceous, often overlapping, to 15 cm long, apex long and tapering, not dry or brown. *Inflorescence* several flowered, inner spathe 14–18 cm long, outer several cm shorter, entirely herbaceous or with a dry brown apex. *Flower* pale yellow to grey veined with mauve, especially on crests, self-colored or distinctly blotched with mauve at the base; *outer perianth segments* 6–7.5 cm long, limb to 4.5 cm long and to 3 cm wide; ovate with tapering claw; *inner segments* lanceolate 4–5 cm long and up to 1.5 cm wide. *Filaments* 0.8–1.2 cm long, joined in lower half; *anthers* about 1.3 cm long. *Style* 4 mm, branches to 2 cm, crests 1–1.5 cm, flushed with mauve. *Ovary* about 2 cm long; *capsule* to 3 cm long, depressed, disciform. *Chromosome number* (subsp. *graminicola*) $2n = 12$, *Mauve 4466* (PRE).

Icon: Obermeyer, Fl. Pl. Africa 39: *Pl. 1526.* 1969. (= subsp. *graminicola.*)

Two subspecies are recognised, the typical form occurring in Natal, flowering early, often before the spring rains, and a second form, to the south in the Transkei. In the latter area plants are generally taller and tend to flower later. Both subspecies are found in open grassland and are solitary.

KEY TO THE SUBSPECIES

1. Bract leaves 1 or 2; stigmas not darkly blotched at base; occurring in Natal ..... a. subsp. *graminicola*

1′. Bract leaves 3; stigmas darkly blotched at base; occurring in the Transkei .... b. subsp. *notata*

21a. subsp. **graminicola**

Plants seldom exceeding 45 cm. *Scape* unbranched, bearing 1 to 2 overlapping bract leaves. *Flowers* pale yellow to grey, veined with mauve; *style crest* sometimes flushed a pale mauve, but not darkly marked at the base.

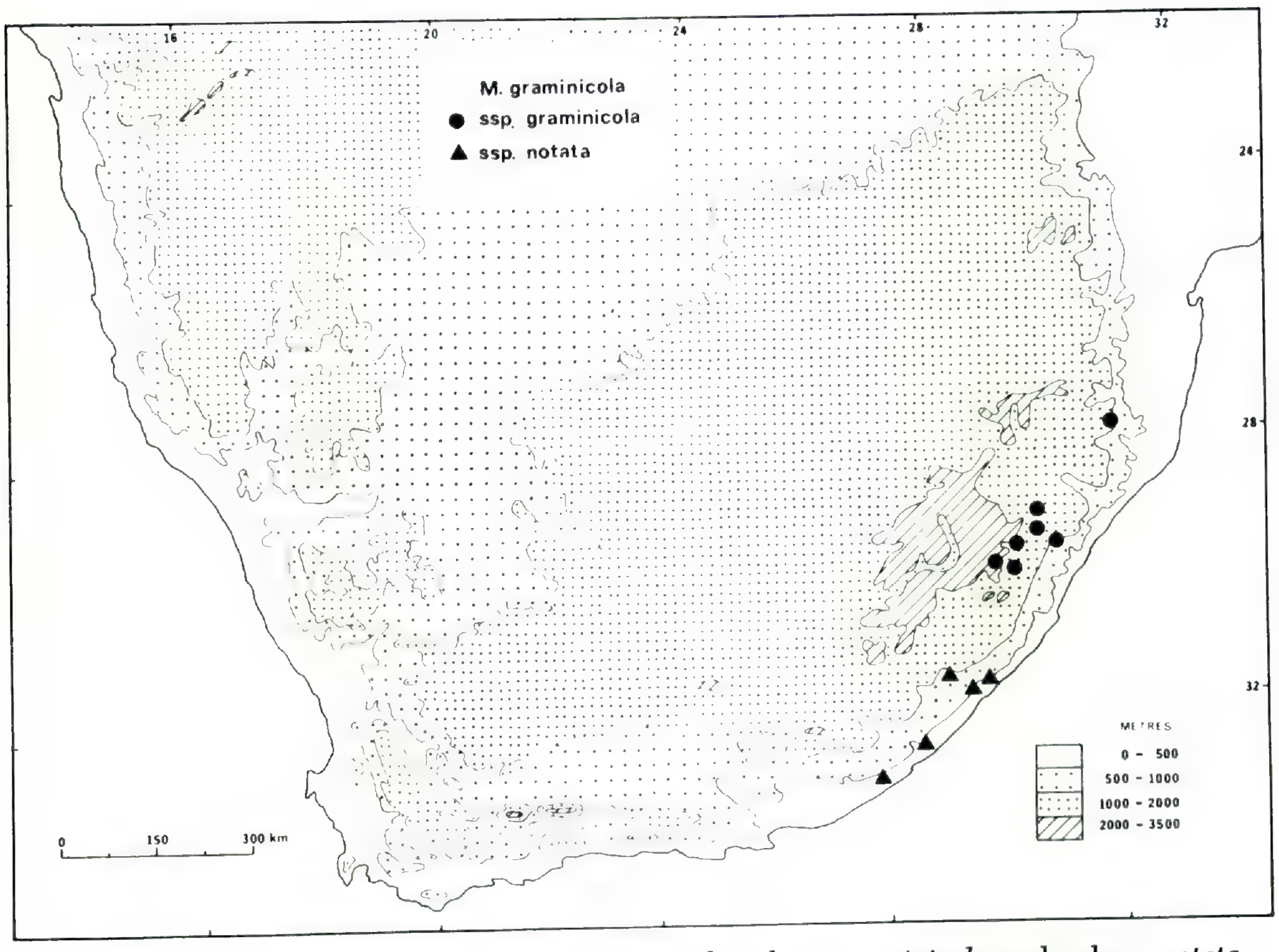

FIGURE 13. Distribution of *Moraea graminicola* subsp. *graminicola* and subsp. *notata*.

Flowering time: August to November.
Distribution: Grasslands in central Natal (Fig. 13).

This subspecies is fairly well known and has been fully described, with ecological observations, in *Flowering Plants of Africa*, where a good illustration can be found.

27.31 (Louwsburg): Near Ngome (-CD), *Gerstner 4876* (PRE).
29.29 (Underberg): Near Underberg (-C), *Dyer 3265* (PRE); Everglades, Impendle district (-DB), *Moll 1259* (NU, PRE); near Bulwer station (-DD), *Killick & Marais 2098* (PRE).
29.30 (Pietermaritzburg): Clovelly farm, Mooi River (-AA), *Mauve 4466* (BOL, PRE); Nottingham Road (-AC), *Galpin 9442* (PRE); Hilton road (-CB), *Williams s. n.* (PRE).

21b. subsp. **notata** Goldbl., subsp. nov. Type: East of Libode, *Codd 10691* (BOL, holotype, PRE, isotype).

Planta 40–60 cm alta, plerumque grandior quam subsp. *graminicola*. *Scapus* simplex, raro ramosus. *Folia vaginantia* plerumque 3. *Flores* pallidi lutei, aut cremei. *Cristae styli* notatae brunneo-purpureo colore.

Plants 40–60 cm high, usually larger than subsp. *graminicola*. *Scape* simple or occasionally branched; bearing 3 bract leaves. *Flowers* pale yellow to cream; *style crest* marked at base a dark brown to mauve color.

Flowering time: September to January.
Distribution: Grasslands in the Transkei (Fig. 13).

This plant, here accorded subspecific rank, is very like the typical *Moraea*

graminicola, as can be seen from its similar, pale rather truncate, submembranous prophylls (Fig. 2C). It is usually later flowering than subsp. *graminicola* and, from the few collections seen, is a generally more robust plant. It is very easy to recognise by the characteristic dark marking at the base of the style crests, a feature otherwise known only in *M. huttonii*, a species growing in large clumps along streams or in other moist situations.

Moraea graminicola needs more investigation before the present treatment can be validated; subsp. *graminicola* is fairly well known in a limited area of Natal, but it probably occurs outside this area. Southern Natal and Pondoland particularly should be surveyed for this species, and it is possible that forms intermediate between the two subspecies will be found in this intervening area between the known ranges for each subspecies.

31.28 (Umtata): Umtata (-DB), *Barker s. n.* (NBG 58666).

31.29 (Port St. Johns): 80 km SE of Umtata (-C), *Reynolds 3037* (PRE); E of Libode (-CB), *Codd 10691* (BOL, PRE); Mlengana Pass, *Schelpe 5026* (BOL, SAM); 12 km N of Umzimvubu River (-DA), *Theron 1555* (BOL).

32.28 (Butterworth): Near Kei River mouth (-CB), *Flanagan 1072* (BOL, PRE); *Compton 17646* (NBG).

33.27 (Peddie): East London (-BB), *Peacock s. n.* (SAM 65682).

22. **Moraea galpinii** (Bak.) N. E. Br., Trans. Roy. Soc. S. Africa 18: 346. 1929. —FIG. 2D.

Moraea spathacea var. *galpinii* Bak., Fl. Cap. 6: 14. 1896. Type: *Galpin 459*, Saddleback range (K, holotype, PRE, BOL, isotypes).

Plant reaching to 30 cm above ground, solitary or in small clumps. *Corm* to 1.8 cm in diameter, covered by fibrous remains of tunics of previous seasons. *Prophylls* (of flowering stem) dark brown to black, fairly rigid vertical fibres often reaching above the ground (fibres of previous seasons often present). *Basal leaf* present or absent at flowering time, eventually exceeding the inflorescence; canaliculate to terete with adaxial groove, 1–10 mm wide. *Scape* erect, unbranched. *Bract leaves* usually 3 or 4, rarely 2, 6–8 cm long, usually overlapping. *Inflorescence* several-flowered, inner spathe to 11 cm long, outer about 7 cm. *Flower* yellow with orange-gold nectar guides; *outer perianth* segments 4–6.5 cm long, limb to 4 cm long and 2.2 cm broad, obtuse to retuse; *inner perianth segments* lanceolate, to 5 cm long and about 1 cm broad; obtuse to retuse. *Filaments* to 8 mm long, joined for two-thirds of length; *anthers* to 9 mm. *Style* 6 mm long, branches to 1.3 cm, crests 1–1.5 cm long. *Ovary* about 1 cm long, extending to 2 or 2.5 cm as flower wilts.

Flowering time: August to early November.

Distribution: Rocky hill slopes from Mt. Anderson to East Griqualand (Fig. 14).

Icon: Obermeyer, Fl. Pl. Africa 40: *Tab. 1582.* 1970. (= subsp. *galpinii.*)

Moraea galpinii can be recognised by its distinctive, firm prophylls, which are dark colored and divided into fairly thick vertical fibres. These tend to persist, and they form a dense layer round the base of the plant (Fig. 2D). It is strange to note that immature plants, *i. e.* those not yet at flowering age, have quite different, soft, entire, membranous prophylls.

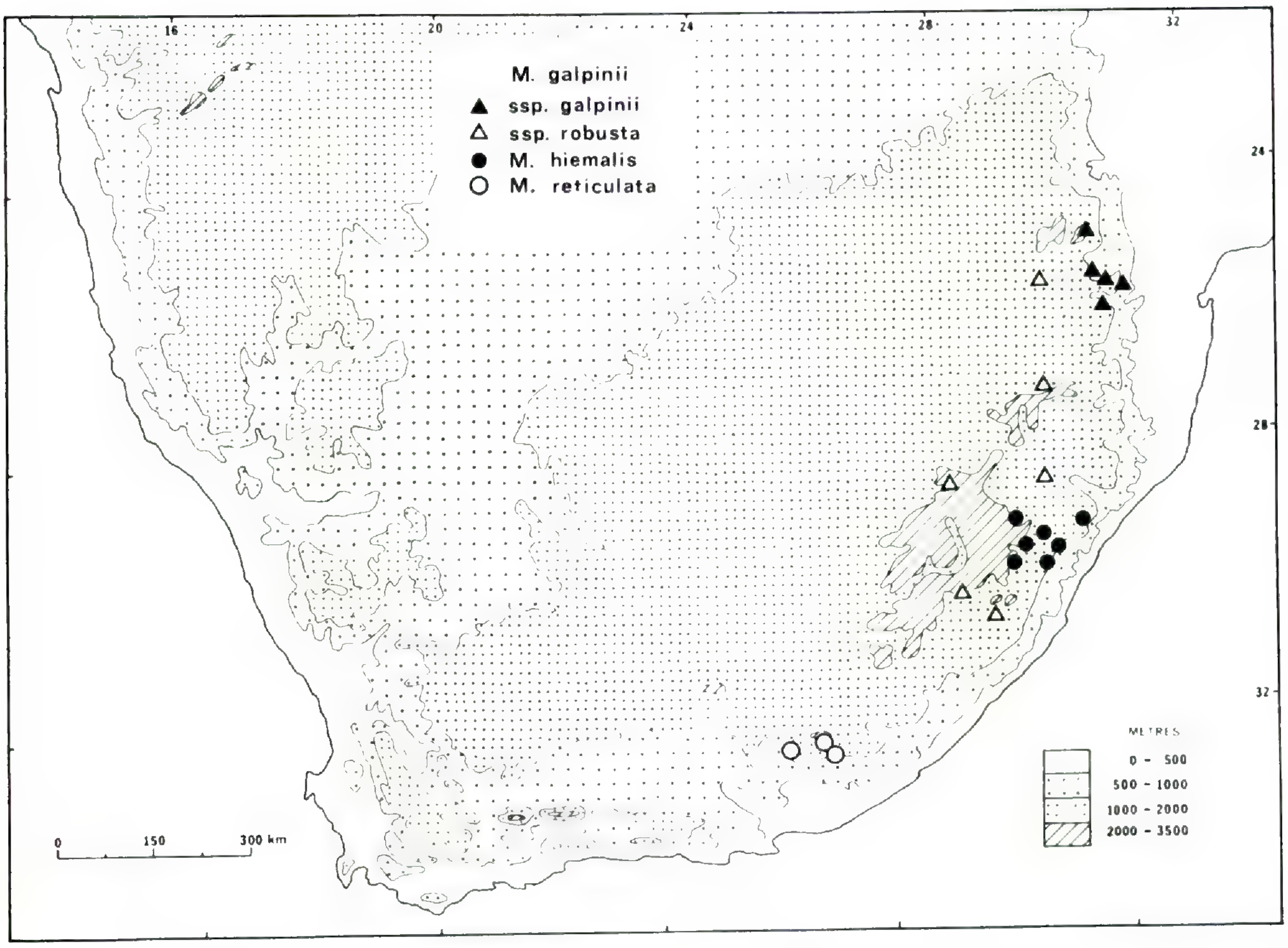

FIGURE 14. Distribution of *Moraea galpinii* subsp. *galpinii* and subsp. *robusta*, *M. hiemalis*, and *M. reticulata*.

Moraea galpinii is itself one of the smaller flowered members of the *Grandiflora* group, though some plants referred to subsp. *robusta* may be quite large. Plants flower early in spring, often before the first rains, and sometimes flowers appear before the leaf is evident. Whether this is due to veld burning, which destroys the apex of the emergent leaf, or whether it really does develop late in some seasons, is not clear.

There appear to be discrete forms of *Moraea galpinii*, the typical one found locally around Barberton and extending south into the adjacent areas of Swaziland and north to Mt. Anderson, and a second more robust form which is widespread, occurring from the Belfast-Machadodorp area of the Transvaal to the Eastern Cape. The second form has not often been collected, and very little is known about it. The structure of the prophylls is, however, so distinctive that there is no doubt it is part of the *M. galpinii* complex. It is with some hesitation that this species is treated as comprising two subspecies, but this is the most acceptable in the present state of our knowledge.

KEY TO THE SUBSPECIES

1. Leaf terete with adaxial groove, 1–2.5 mm in diameter; outer perianth segments to 4 cm long ---------- a. subsp. *galpinii*
1′. Leaf canaliculate to flat, more than 2.5 mm wide; outer perianth segments to 6.5 cm long ---------- b. subsp. *robusta*

22a. subsp. **galpinii**

Plants smaller than subsp. *robusta*, to 30 cm high. *Basal leaf* present or not yet developed at flowering time, eventually exceeding the inflorescence, terete to 2.5 mm wide. *Bract leaves* 3, rarely 2 or 4. *Flowers* yellow; *outer perianth segments* up to 5 cm long.

Flowering time: August to early October.

Distribution: Rocky mountain slopes between Mt. Anderson and Mbabane (Fig. 14).

Moraea galpinii was first described by Baker as a variety of *M. spathulata* (as *spathacea*) and was elevated to specific rank by N. E. Brown in 1929. Although at first it was known only from very limited material, it has now become clear that it is a fairly common and widespread species. The typical subspecies is well understood, having been rediscovered by Mrs. A. A. Mauve, who described it in *Flowering Plants of Africa* in 1969.

25.30 (Lydenburg): Long Tom Pass (-BA), *Rauch & Schlieben 9774* (PRE); Mount Anderson, *Humbert 10957* (P); Kaapsche Hoop (-DB), *Rogers s. n.* (BOL 30817, PRE 18815).
25.31 (Komatipoort): Barberton (-CC), *Thorncroft s. n.* (GRA 25516, PRE 25972); near Havelock Mine, *Mauve 4802* (PRE); Saddleback Range, *Galpin 459* (BOL, PRE); 27 km SE of Barberton (-CD), *Codd 1621* (PRE).
26.31 (Mbabane): Forbes Reef (-AA), *Compton 26942* (PRE); *Compton 27979* (NBG).

22b. subsp. **robusta** Goldbl., subsp. nov. Type: Naauwhoek, Utrecht district, *Devenish 109* (PRE, holotype).

Planta grandior quam subsp. *galpinii*, ad 40 cm alta. *Folium basale* canaliculatum aut subteres 3–10 mm latum. *Foli vaginantia* 3–4. *Flores* pallidi lutei ad albi; *perianthii segmenta exteriora* plerumque longiora quam subsp. *galpinii*, ad 6.5 cm longa.

Plants larger than subsp. *galpinii*, to 40 cm high. *Basal leaf* canaliculate to subterete and 3–10 mm wide. *Bract leaves* 3–4. *Flowers* pale yellow, to white; *outer perianth segments* usually longer than subsp. *galpinii*, up to 6.5 cm long.

Flowering time: August to mid-November.

Distribution: Eastern Transvaal to eastern Cape (Fig. 14).

As already mentioned, this subspecies is not fully understood, but represents the somewhat more robust, larger flowered group with fibrous corm tunics exactly like those of typical *Moraea galpinii*. It can be distinguished from subsp. *galpinii* by its larger flower and leaf, which is canaliculate or subterete, but wider than the terete leaf of subsp. *galpinii*.

25.30 (Lydenburg): Near Machadodorp (-CA), *Grosser s. n.* (PRE 1607).
27.30 (Vryheid): Naauwhoek, Utrecht district (-AC), *Devenish 109* (PRE); Oshoek, Wakkerstroom, *Mauve 4486* (PRE).
28.28 (Bethlehem): Near General Will Hill (-DA), *Liebenberg 7324* (PRE).
28.30 (Dundee): Kafir Drift, Utrecht (-CA), *Thode 363A* (NH).
30.28 (Matatiele): Quachasnek (-BB), *Strey 4318* (NH).
30.29 (Kokstad): Kokstad (-CB), *Goodall s. n.* (BOL 8278).

23. **Moraea hiemalis** Goldbl., sp. nov. Type: Lions River, *Obermeyer s. n.* (PRE 33562, holotype).

Planta ad 45 cm alta, solitaria. *Cormus* 1 cm diam. *Prophylla* brunneum, fragile, integrum aut fractum irregulariter, argenteum et purpureum infra. *Folium basale* excedens inflorescentiam, teres. *Scapus* erectus simplex. *Folia vaginantia* 3–5, imbricata, ad 14 cm longa.

Inflorescentia pluriflora, spatha interior 4–8 cm longa, exterior aequalis aut brevior. *Flores* lutei; *perianthii segmenta exteriora* ad 5 cm longa, limbus ad 3.5 cm longus et ad 2.4 cm latus; *segmenta interiora* ad 4 cm longa et 1.5 cm lata. *Filamenta* ad 8 mm longa, *antherae* ad 1 cm longae. *Stylus* circa 4 mm longus, rami ad 1.3 cm longi, cristae circa 1 cm longae. *Germen* circa 1.5 cm longum, *capsula* 2–2.5 cm longa.

Plants to 45 cm high, solitary. *Corm* about 1 cm in diameter, tunics not known. *Prophylls* brown, brittle, entire, or irregularly broken, ribbed and silver and purplish below. *Basal leaf* over-topping inflorescence, margins tightly inrolled (terete in section), about 5 mm in diameter, unopened. *Scape* erect, simple. *Bract leaves* (3–)4–5, overlapping, to 14 cm long. *Inflorescence* several-flowered, inner spathe 8–14 cm, outer equal or slightly shorter; herbaceous, with dry light brown apex. *Flower* yellow, darkly veined; *outer perianth* segments to about 5 cm long, limb to 3.5 cm long and to 2.4 cm wide; *inner segments* erect to about 4 cm long and 1.5 cm wide. *Filaments* to 8 mm long, free in upper third; *anthers* to 1 cm long. *Style* about 4 mm long, branches to 1.3 cm long, crests about 1 cm long. *Ovary* about 1.5 cm long. *Capsule* 2–2.5 cm long and about 1 cm wide.

Flowering time: July to August.

Distribution: Grassland in central Natal (Fig. 14).

Moraea hiemalis is a distinct segregate of the *M. spathulata* complex and is accorded specific rank. It is isolated by its flowering time from representatives of *M. spathulata* in the same area, as it flowers in July and August, while *M. spathulata* flowers later, from October onwards. Morphologically it can be distinguished by its terete leaf, the margins being tightly inrolled, and its solitary habit. The plants are also generally smaller in most features than typical *M. spathulata.*

29.29 (Underberg): Near Mooi River (-B) *Schlechter 3340* (BOL); Boston, Impendhle (-DB), *Beattie 40* (NU); Bulwer (-DC), *Gerstner s. n.* (NH 28756).

29.30 (Pietermaritzburg): Michael House (-AC), *Strey 3867* (NH, PRE); Balgowan, *Obermeyer s. n.* (PRE 33562); Elandskop (-BB), *Gibson s. n.* (NH 17300); Umgeni Poort (-CA), *Moll 957* (NU); Winters Kloff (-CB), *Wilson s. n.* (NH 17123); Hilton road, *Garbutt 36* (NU); World's View, *Douwes-Dekker 2* (NU); Town Hill, *Barker 3579* (NBG); 8 km E of Richmond (-CC), *Strauss 204* (NBG).

24. **Moraea reticulata** Goldbl., sp. nov. Type: Top of Katberg Pass, *Goldblatt 682* (BOL, holotype, MO, PRE, isotypes).

Planta solitaria raro caespitosula. *Cormus* ad 2 cm diam., munitus fibris. *Prophylla* fibrosa, reticulata interior ad 20 cm altum vaginans folium et scapum. *Folium basale* solitarium, canaliculatum, ad 1.5 cm latum, scapum excedens. *Scapus* 45–70 cm altus, erectus, simplex. *Folia vaginantia* 3–4, herbacea aut membranescentia in senectute ad 15 cm longa. *Inflorescentia* ad 15 cm longa, spatha exterior aliquantum brevior quam interior. *Flores* lutei; *perianthii segmenta exteriora* ad 7 cm longa et circa 2.5 cm lata; *segmenta interiora* 5–6 cm longa, ad 1.5 cm lata. *Filamenta* ad 1.3 cm longa, connata in parte inferiore; *antherae* lineares, albi, ad 1.5 cm longae. *Rami styli* ad 2 cm longi, cristae aliquantum breviores. *Germen* linear, 2–3 cm longum. *Capsula* ad 4 cm longa; *semina* disciformia.

Plants solitary, rarely in small clumps. *Corm* to 2 cm in diameter, covered by the decayed leaf bases and prophylls of previous seasons. *Prophylls* fibrous, reticulate, inner produced to 20 cm above ground in a network, sheathing leaf and scape. *Basal leaf* solitary, canaliculate (conduplicate when dry), to 1.5 cm wide, exceeding the scape. *Scape* 45–70 cm long, erect, simple. *Bract leaves* 3–4, green, becoming membranous late in season, to 15 cm long. *Inflorescence*

about 15 cm long, outer spathe slightly shorter than inner. *Flowers* bright yellow with orange nectar guide; *outer perianth segments* to 7 cm long and about 2.5 cm wide; *inner segments* 5–6 cm long and to 1.5 cm wide. *Filaments* to 1.3 cm long, joined in lower half; *anthers* linear, white, to 1.5 cm long. *Style branches* about 2 cm long, crests somewhat shorter. *Ovary* linear, 2–3 cm long. *Capsule* to 4 cm long; *seeds* depressed, disciform.

Flowering time: March to May.

Distribution: Amatola Mountains between Bedford and Cathcart, eastern Cape (Fig. 14).

The flowers of *Moraea reticulata* are similar to those of *M. spathulata*, but the plants themselves differ in being almost invariably solitary. True *Moraea spathulata* has been recorded from the same locality as *M. reticulata* where the former flowers in late spring or summer, while *M. reticulata* flowers in autumn, from March to May.

Moraea reticulata can always be recognised by its very characteristic prophylls, the inner one of which extends upwards well above the ground and forms a grey or brown network around the leaf and stem. This type of prophyll is found in some forms of *M. spathulata* but is never as strongly developed, and it also occurs in *M. alticola*. In the latter species, which is found at high altitudes in the Drakensberg, the reticulate prophyll is also strongly developed and often yellow. *Moraea reticulata* can, however, be easily distinguished from *M. alticola* as the latter grows in clumps and has broad, flat leaves in contrast to the canaliculate leaves of *M. reticulata*.

Moraea reticulata is, like *M. hiemalis*, a distinct segregate of the *Moraea spathulata* complex. Both the former species have been given specific rank, although it is clear that they are very closely allied to *M. spathulata*. The decision to accord them specific rank is based partly on their solitary habit and partly because they flower at quite different seasons from the forms of *M. spathulata* found in the same areas.

In contrast, the subspecies of *Moraea spathulata* flower at more or less the same time, or the flowering period grades from winter to summer, depending on decreasing latitude or differences in altitude. The subspecies *autumnalis* is an exception for it flowers later than other subspecies of *M. spathulata*. In this case, however, the caespitose habit of subsp. *autumnalis* has been regarded as indicative of close relationship with *M. spathulata*.

32.26 (Fort Beaufort): Bedford district (-CA), *Jeppe 850* (GRA); Baviaansrivierberg, Bedford, *Killick 850* (PRE); top of Katberg Pass (-DB), *Goldblatt 682* (BOL, MO, PRE); Hogsback, *Lewis 4422* (SAM); *Lubke & Jacot-Guillarmod 5632* (RUH); Happy Valley, Hogsback, *Johnson 1258* (GRA).

25. **Moraea spathulata** (L. f.) Klatt *in* Dur. & Schinz, Consp. Fl. Afr. 5: 152. 1895.

Iris spathulata L. f., Suppl. 99. 1781. Type: Wolwekraal, Langekloof, *Thunberg* in Herb. Thb. 1172 (UPS, holotype).

Plants to 1 m high, usually in clumps, rarely solitary. *Corm* to 2 cm in diameter, frequently covered by fibrous remains of old tunics and leaf bases.

Prophylls brown to pale straw, membranous to firm, entire or irregularly broken, or splitting into a fibrous reticulum above. *Basal leaf* overtopping stem, linear, flat to curved to canaliculate. *Scape* occasionally branched. *Bract leaves* herbaceous, 3–5, often overlapping, 9–18 cm long, apex dry, brownish. *Inflorescence* several-flowered, inner spathe 10–18 cm, outer a little shorter. *Flowers* deep to pale yellow with prominent veins, nectar guides deeper yellow-orange; *outer perianth segments* 3.5–7.5 cm long, limb to 4 cm long and about 2.5 cm wide; *inner segments* 3–6 cm long, less than 2 cm wide. *Filaments* 8–15 mm, joined in lower part; *anthers* 7–15 mm, purple. *Style* 2–3 cm long. *Capsule* to 5 cm long; *seeds* depressed, disciform.

Icones: Batten & Bokelmann, Wild Flowers of the Eastern Cape Province. *Pl. 28, fig. 1.* 1966; Courtenay-Latimer *et al.*, The Flowering Plants of the Tsitsikama Forest and Coastal National Park. *Pl. 18, fig.* 5. 1967.

Moraea spathulata is a widespread species of extremely variable nature. It occurs from the George district in the southern Cape where it flowers in winter to southern Zululand, the slopes of the Natal Drakensberg, and the Transvaal and Swaziland mountain areas where it may flower in summer or autumn. The species can be distinguished by its large bright yellow flowers, tall stems, and caespitose habit. It comprises numerous local races, but owing to the small and gradual differences between them, it is difficult to define many races. However, four subspecies are recognised here as distinct. Two other close allies of this species, *M. hiemalis* and *M. reticulata*, have been accorded specific rank (see discussion under *M. reticulata*).

Key to the Subspecies

1. Prophylls pale, submembranous, entire or frayed at apex, but not fibrous or reticulate; outer perianth segments rarely exceeding 5 cm; solitary or small clumps among rocks on hilltops in eastern Transvaal, Swaziland ..... c. subsp. *saxosa*

1′. Prophylls brown, firm, entire or irregularly broken or becoming fibrous with age and sometimes forming a reticulum above; outer perianth segments rarely less than 5 cm; in clumps (rarely solitary) southern Cape to eastern Transvaal.

2. Prophylls occasionally forming a reticulum above, it not, leaves less than 1 cm wide or canaliculate; occurring in Natal, Orange Free State, Cape Province.

3. Flowering in autumn in eastern Cape, southern Natal ..... d. subsp. *autumnalis*

3′. Flowering in late winter, spring or summer in Cape Province, Orange Free State or Natal ..... a. subsp. *spathulata*

2′. Prophylls not forming fibrous network above; leaf flat or curved (rarely canaliculate); occurring in eastern Transvaal, Swaziland, often associated with forest margin ..... b. subsp. *transvaalensis*

25a. subsp. **spathulata**—Fig. 3B.

Moraea spathulata (L. f.) Klatt, Dur. & Schinz., Consp. Fl. Afr. 5: 152. 1895.
Iris spathulata L. f., Suppl. 99. 1781. Type: Wolwekraal, Langkloof near Keurbooms River, *Thunberg* in Herb. Thunb. *1172* (UPS, holotype).
Iris spathacea Thunb., Diss. Iride no. 23. 1872. Type: Wolwekraal, Langkloof, *Thunberg* in Herb. Thunb. *1172* (UPS, holotype).
Moraea spathacea (Thunb.) Ker., Bot. Mag. *Tab 1103.* 1808, *non* Thunb. (1787).
Moraea longispatha Klatt, Linnaea 34: 560 (1866). Type: Banks of Kei River, "Tambukiland," *Ecklon & Zeyher* (Irid. 3) (MO, isotype).

Plants in large clumps, rarely solitary. *Prophylls* dark brown, brittle, becoming fibrous, extending above ground as a dark colored network. *Leaf* flat to

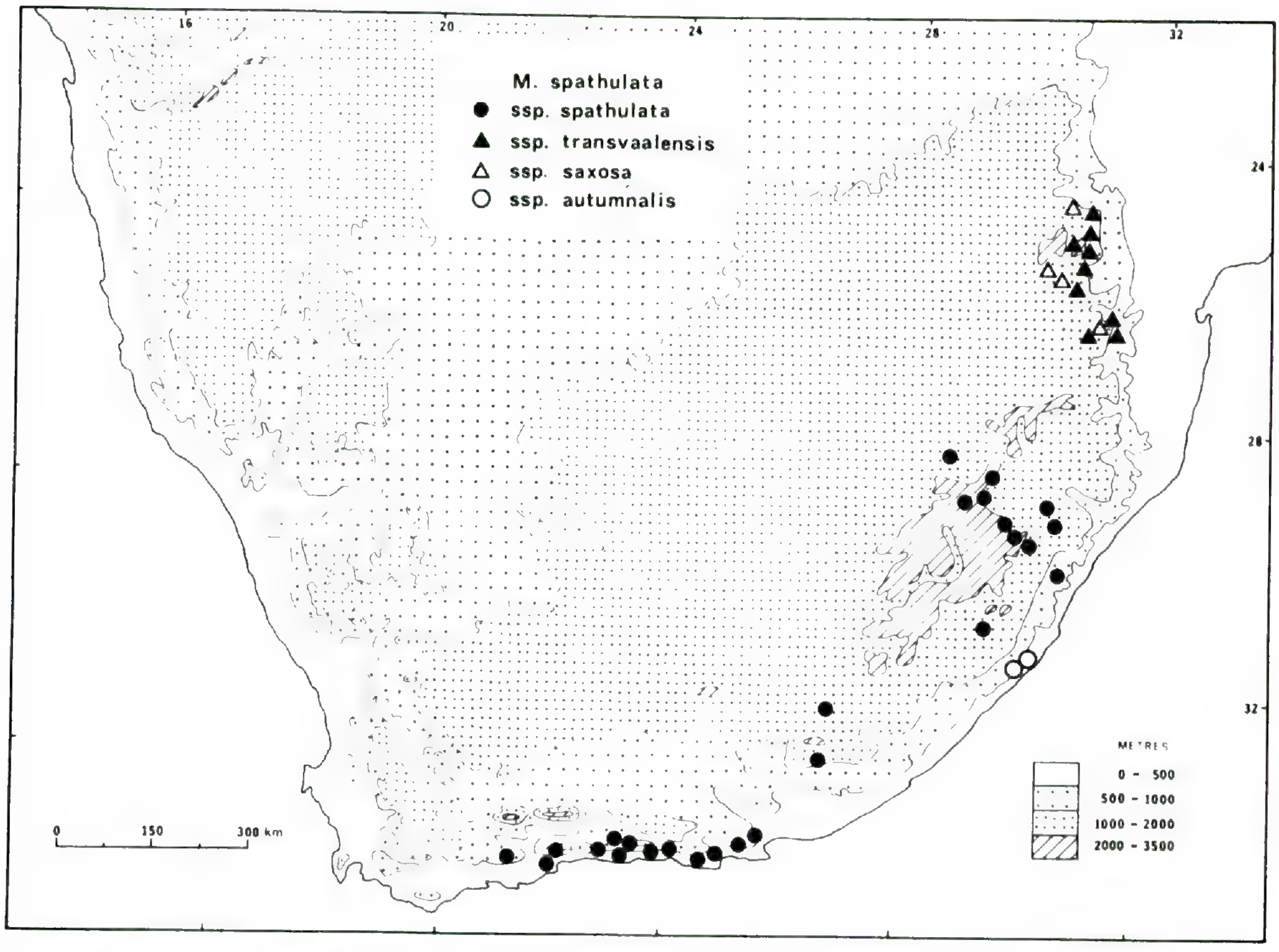

FIGURE 15. Distribution of *Moraea spathulata* and its subspecies.

canaliculate, 1–2.5 cm wide, green to glaucous. *Scape* simple or occasionally 1–2 branched. *Flowers* pale to deep yellow with darker nectar guides; *outer perianth segments* to 7 cm long; *inner segments* to 5.5 cm long. *Filaments* about 1 cm long, free in upper half; *anthers* about 1 cm long. *Style* about 5 mm with branches reaching 1.5–2 cm long, crests to 1.5 cm long. *Ovary* about 2 cm long; *capsule* 4–4.5 cm. *Chromosome number* $2n = 12$, *Naude s. n.* (PRE 30038); *Goldblatt 26* (J).

Flowering time July to November.

Distribution: Southern and eastern Cape, Orange Free State and Natal (Fig. 15).

This, the most variable of the four subspecies of *Moraea spathulata*, is also the most widespread. It is found from the George area of the southern Cape, where it is winter or early spring flowering, to southern Zululand and the Drakensberg slopes. It generally flowers in late spring in the latter areas. Plants of subsp. *spathulata* from the southern Cape coastal areas have the broadest leaves and the most fibrous corm coverings. Those occurring at higher altitudes are generally smaller and have more slender leaves, while forms in central Natal and southern Zululand tend to be variable, some races only being characterised by a rather bare stem instead of being covered by overlapping bracts.

Subspecies *spathulata* may be found on further examination to consist of several distinct varieties or subspecies, especially among the more slender mountain forms in Natal. The author has, however, found it impossible to suc-

cessfully draw the line between different forms as the variation between and among populations seems too inconsistent. With more study, particularly of live populations, a better understanding of the subspecies should be achieved.

28.28 (Bethlehem): Kestell (-BA), *Strey 9073* (NH); near Sentinel Gate (-DD), *Killick & Marais 2207* (PRE).

28.29 (Harrismith): Rensburgskop (-AD), *Jacobsz 292* (PRE); Bergville district (-C), *Killick & Marais 2139* (PRE).

28.31 (Nkandla): Near Eshowe (-CD), *Lawn 1116* (NH); *Gerstner 2423* (NH).

29.29 (Underberg): De Hoek, Estcourt District (-B), *Quail s. n.* (NH 5341); Tabamhlope (-BA), *Wood 10641* (NH); Nottingham Road (-BD), *Wood 5182* (NH, PRE).

29.30 (Pietermaritzburg): Howick (-AC), *Thomas s. n.* (NBG 58663); Greytown (-BA), *Wylie s. n.* (NH 21676); near Bothas Hill (-DC), *Wood 8650* (NH).

30.29 (Kokstad): Kotstad, hill tops, *Mogg 1795* (PRE); near Kokstad (-CB) *Haygarth s. n.* (NH 4183).

31.26 (Queenstown): Queenstown district (-D) *Galpin 1576* (GRA). Buffelsfontein, Halseton, *Stretton s. n.* (NBG 2902).

32.26 (Fort Beaufort): Katberg (-DA), *Dyer 789* (GRA).

33.21 (Ladismith): Garcia's Pass (-CC), *Leipoldt s. n.* (BOL 16057).

33.22 (Outdtshoorn): George (-CD), *Young s. n.* (BOL 5544), 38 km E of George (-DD), *Baker s. n.* (PRE); near Barrington, *Salter 6920* (BOL).

33.23 (Willowmore): Avontuur (-CA), *Fries, Norlindh & Weimarck 1533* (LD, PRE, SAM); Misgund-Avontuur (-CB), *Fourcade 434A* (BOL); S of Avontuur (-CC), *Mauve 4605* (PRE); Deepwalls Forest, *Horn s. n.* (PRE); near Keurboomsrivier (-DC), *Thompson 876* (PRE); *Loubser 875* (NBG).

33.24 (Steytlerville): Oudebosch (-CC), *Fourcade 868* (GRA).

33.25 (Port Elizabeth): Greenbushes (-CD), *Long 639* (PRE); Uitenhage, *Batten 1* (NBG).

34.22 (Mossel Bay): Pacaltsdorp (-AB), *Thorne s. n.* (SAM 51706).

34.24 (Humansdorp): Clarkson (-AB), *Cassidy 235* (NBG); Humansdorp (-B), *Rogers 2884* (PRE).

25b. subsp. **transvaalensis** Goldbl., subsp. nov. Type: Near Sabie Transvaal, *Goldblatt 610* (BOL, holotype, MO, isotype).—Fig. 2B.

Planta caespitosa (raro solitaria). *Prophylla* brunnea, saepe argenteo et purpureo colore striata ad basem, fragilia, integra aut irregulariter fracta, raro fibrosa supra. *Folia* 1–2.5 cm lata, plana aut parum concava. *Scapus* simplex. *Flores* pallidi lutei; *perianthii segmenta exteriora* 6–7.5 cm longa; *segmenta interiora* ad 6 cm longa. *Filamenta* circa 1.5 cm longa, *antherae* 1.2–1.4 cm, nigrae. *Stylus* ad 7 mm longus, rami ad 2 cm longi, cristae ad 1.5 cm longae. *Germen* circa 2–2.5 cm longum; *capsula* ad 4 cm longa.

Plants growing in large clumps. *Prophylls* brown, brittle, entire or irregularly broken, occasionally fibrous above. *Leaves* 1–2.5 cm wide,flat or slightly concave. *Scape* simple. *Flowers* very pale yellow; *outer perianth segments* 6–7.5 cm long, occasionally shorter; *inner segments* up to 6 cm long. *Filaments* about 1.5 cm long; *anthers* 1.2–1.4 cm long, black. *Style* about 7 mm long, branches to 2 cm long and crests about 1.5 cm long. *Ovary* 2–2.5 cm long; *capsule* 4 cm long. *Chromosome number* $2n = 12$, *Goldblatt 14* (J).

Flowering time: Late summer to autumn (December to March).

Distribution: Eastern Transvaal and Swaziland mountains (Fig. 15).

Subspecies *transvaalensis* is a distinct segregate of the *Moraea spathulata* complex occurring in the eastern Transvaal and Swaziland mountain regions. It grows in large clumps, usually on the verge of forests or thick bush.

24.30 (Pilgrim's Rest): Mariepskop (-DD), *van der Schyff 4553* (PRE); Mac Mac Falls area (-DD), *Goldblatt s. n.* (PRE 31508).

25.30 (Lydenburg): 8 km E of Lydenburg (-BA), *Obermeyer s. n.* (PRE 36286); Sabie valley (-BB), *Galpin 13587* (PRE); near Sabie, *Codd 9487* (PRE); *Goldblatt 610* (BOL, MO); Rosehaugh (-BD), *Mogg 13676* (PRE); Kaapsche Hoop (-DA), *Rogers 21048* (NH).
26.30 (Carolina): Little Usutu valley (-BD), *Compton 25400* (NBG, PRE).
26.31 (Mbabane): Gobolo, Mbabane (-A), *Compton 30349* (NBG); Komati Pass, *Compton 29643* (NBG); near Mbabane (-AC), *Compton 25066* (PRE).

25c. subsp. **saxosa** Goldbl., subsp. nov. Type: Summit of Long Tom Pass, *Goldblatt 612* (BOL, holotype, PRE, isotype).

Planta caespitosa aut solitaria inter saxa et in rimis. *Prophylla* pallida, submembranacea, integra aut ad apicem lacerata, sed non fibrosa. *Folia* atroviridia, plana aut parum concava, 0.6–1.5 cm lata. *Scapus* simplex. *Flores* lutei; *perianthii segmenta exteriora* 3.5–4.5 (–5.0) cm longa; *segmenta interiora* ad 3.5 cm longa. *Filamenta* ad 1 cm longa; *antherae* 7–9 mm longae. *Stylus* circa 6 mm longus, rami ad 1 cm longi, cristae ad 8 mm longae. *Germen* 2–3 cm longum, *capsula* 5 cm longa.

Plants growing in small clumps or solitary in rock crevices or among boulders. *Prophylls* pale, submembranous and entire or frayed at apex, but not fibrous. *Leaves* dark green, flat or slightly concave, 0.6–1.5 cm wide. *Scape* simple. *Flowers* bright yellow with a deeper yellow nectar guide; *outer perianth segments* 3.5–4.5(–5.0) cm long; *inner segments* up to 3.5 cm long. *Filaments* about 1 cm long, *anthers* 7–9 mm long. *Style* about 6 mm long, branches to 1 cm and crests about 8 mm long. *Ovary* 2–3 cm long; *capsule* 5 cm long.

Flowering time: December to February.

Distribution: Exposed rocky hilltops in the eastern Transvaal Drakensberg (Fig. 15).

This subspecies is smaller in all its characters than other forms or subspecies of *Moraea spathulata*, with the exception of the size of the capsule which is the largest in the *spathulata* complex. As mentioned, subsp. *saxosa* occurs on exposed rocky hills at various altitudes on the eastern Transvaal Drakensberg escarpment. Unlike most of the other subspecies of *M. spathulata*, the plants can be quite solitary, though they can also form large clumps. It is believed that growing among rocks and in crevices it cannot always achieve the caespitose habit, although it still maintains the potential to do so.

Apart from the reduced size of flower, leaf, and corms, it can be distinguished by its peculiar prophylls which are usually pale, short and soft-textured, similar to those found in *Moraea graminicola*, the latter also a representative of the large flowered *Grandiflora* group.

24.30 (Pilgrim's Rest): Mariepskop (-DB), *Strey 7914* (NH, PRE); *Hilliard & Burtt 5982* (NU); *van Dam s. n.* (PRE 26356); Goedgeloof near Belvedere, *Davidson 527* (J).
25.30 (Lydenburg): Dullstroom, Steenkamps Mountain (-AC), *Galpin 13184* (BOL, PRE); Kemps Heights (-AD), *Codd 8305* (PRE); 16 km E of Sabie (-BA), *Reynolds 2669* (PRE); Long Tom Pass (-BA), *Goldblatt 612* (BOL).
26.31 (Mbabane): Fonteyn, Mbabane (-A), *Compton 31117* (NBG).

25d. subsp. **autumnalis** Goldbl., subsp. nov. Type: Nyameni mouth, Port Edward district, *Strey 8619* (PRE, holotype, NH, isotype).

Prophylla atrobrunnea, fibrascentia aetati, interna pars saepe fibrior in summo. *Folium* ad 1 cm latum, canaliculatum, costatum, prominente in siccis exemplaribus. *Flores* lutei, purpureis venis.

Prophylls dark brown, but white streaked with purple below, becoming fibrous with age; inner sometimes fibrous above. *Leaf* usually less than 1 cm wide, canaliculate, conspicuously ribbed when dry (not seen fresh). *Flowers* yellow, veined with purple.

Flowering time: March to May.

Distribution: Eastern Cape, Transkei, Pondoland (Fig. 15).

As can be seen from the small number of specimens examined, subsp. *autumnalis* is poorly known. The plants resemble other forms of *Moraea spathulata* but have a comparatively narrow, canaliculate leaf; and this, together with its large flower and late flowering habit, suggest that they merit subspecific rank. Like other segregates of *M. spathulata*, the plants are usually found growing in clumps. Subspecies *autumnalis* can be distinguished from the other subspecies of *M. spathulata* by its narrow, prominently ribbed leaf and fibrous corm tunics.

31.30 (Port Edward): Nyameni mouth, Transkei (-AA), *Strey 8619* (NH); S of Port Edward, *Bayliss 2212* (NBG).

26. **Moraea alticola** Goldbl., sp. nov. Type: Mont aux Sources, *Schweickerdt s. n.* (PRE 28588, holotype, NH, isotype).—Fig. 2E.

Planta grandis, ad 1 m alta, caespitosa. *Cormus* ad 2 cm diam., densiter munitus fibris crassis brunneis. *Prophylla* brunnea fracta irregulariter sed facientia pallida, reticulata supra. *Folium* solitarium, excedens scapum, planum, 1.5–3 cm latum marginibus saepe prominentibus. *Scapus* erectus, simplex aut pauciramosus. *Folia* vaginantia 3–5, imbricata, ad 18 cm longa, viridia, apicibus brunneis. *Inflorescentia* pluriflora, spatha interior ad 15 cm longa, exterior aequalis aut brevior. *Flores* lutescentes, *perianthii segmenta exteriora* ad 8 cm longa, limbus ad 5 cm longus, 3–4 cm latus; *segmenta interiora* ad 7 cm longa, erecta. *Filamenta* ad 2 cm longa, connata usque dimidiam partem; *antherae* ad 1.5 cm longae. *Stylus circa* 1.3 cm longus, rami ad 2 cm longi, cristae circa 1.5 cm longae. *Germen* 2–3 cm longum, capsula ad 4.5 cm longa.

Plants large, to 1 m high, in large clumps. *Corm* about 2 cm in diameter, corms and base of stems covered by dark matted fibres of previous season's decayed leaves. *Prophylls* brown, broken irregularly but forming a pale, well developed fibrous network above the ground, sheathing the lower part of the leaf. *Basal leaf* exceeding the inflorescence, broad and flat, 1.5–3 cm wide, margin often thickened and yellow. *Scape* erect, simple or few branched. *Bract leaves* 3–5, overlapping, to 18 cm long, apices brown. *Inflorescence* several flowered, inner spathe 12–15 cm long, outer equal or somewhat shorter. *Flower* pale yellow with darker yellow nectar guide; *outer perianth segments* to 8 cm long, limb to 5 cm long and 3–4 cm wide; *inner segments* to 7 cm long, erect, to 2.5 cm wide. *Filaments* to 2 cm long, joined in lower part, *anthers* about 1.5 cm long, not reaching stigma. *Style* about 1.3 cm long, branches to 2 cm, crests about 1.5 cm long. *Ovary* 2–3 cm long; capsule about 4.5 cm long. *Chromosome number* $2n = 12$, *Trauseld s. n.* (BOL).

Flowering time: Summer, but occasionally from October to March

Distribution: Uppermost slopes and plateau of the Drakensberg in Natal, Cape and Lesotho (Fig. 16).

Moraea alticola, undoubtedly closely allied to *M. spathulata*, has been accorded specific rank, due in part to several distinct and easily recognisable features and to its spatial and ecological isolation from the various forms of *M. spathulata*.

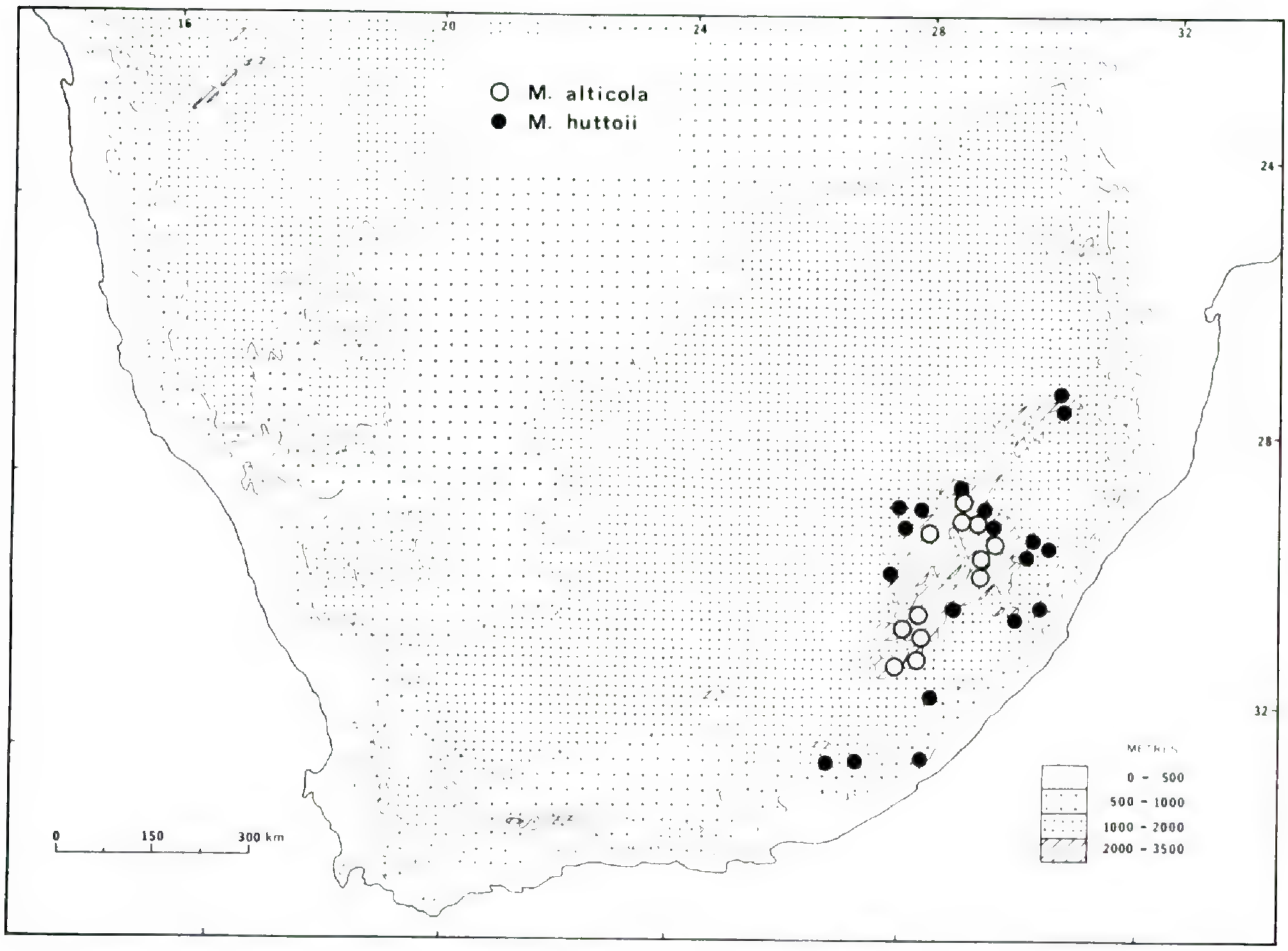

Figure 16. Distribution of *Moraea alticola* and *M. huttonii*.

In spite of its occurring in an alpine area, on the summit plateau of the Drakensberg, it is easily the largest, most robust species in the genus. While size alone makes *M. alticola* easy to distinguish, it can also be very readily recognised by its inner prophyll, which forms a well developed, pale network above the ground (Fig. 2E). Such a feature is found in other allies of *M. spathulata* but never achieves the same degree of development and is often absent in some individuals while present in others in the same population.

28.28 (Bethlehem): Moolman's Hoek Peak, *Galpin s. n.* (BOL 30818); Mont aux Sources (-DD), *Schweickerdt s. n.* (NH 26960, PRE 28588); Royal Natal National Park, *Oliver* 332 (NH); Mont aux Sources, *Schelpe 1409* (NU); Beacon Buttress, *Galpin 10150* (PRE).

28.29 (Harrismith): Cathedral Peak area (-CC), *Schelpe 470* (NU); Cathedral Peak escarpment, *Schelpe 487* (NU); Indumeni Dome, *Killick 1851* (PRE); Cleft Peak area, *Killick & Marais 2186* (BOL, PRE).

28.28 (Marakabei): Mosalamane Pass (-AA), *Jacot-Guillarmod 505* (ROML).

29.29 (Underberg): Giants Castle (-AD), *Bruyns-Haylett 27* (NU), Giants Castle, Gable area, *Trauseld 856* (NU, PRE); Bushman's Pass (-CC), *West 1710* (NH).

30.27 (Lady Grey): Majuba Nek, Sterkspruit (-DB), *Hepburn 289* (GRA).

30.28 (Matatiele): Satsannas Berg (-AC), *Galpin 6845* (PRE); Naudes Nek Pass (-CA), *Story 480* (PRE); Luhana Pass, *Galpin 2322* (BOL, PRE); 8 km W of Naudes Nek (-CC), *Reynolds 3418* (PRE).

31.27 (Lady Frere): Summit, Barkly Pass (-BB), *Rattray s. n.* (PRE 7321).

27. **Moraea huttonii** (Bak.) Oberm., Fl. Pl. Africa *Tab. 1581.* 1970.—Fig. 3A.

Dietes huttonii Bak., Bot. Mag. *Tab. 6174.* 1875. Type: Eastern Cape, *Hutton s. n.* (K, holotype).

Moraea rivularis Schlechter, Bot. Jahrb. Syst. 40: 90. 1908. Type: Ifafa, *Rudatis 100* (B, holotype).
Moraea baurii Bak., Handbook Irid. 50. 1892. Type: Baziya, along streams, *Baur 247* (K, holotype).

Plants large, to 1 m in height, growing in clumps. *Corm* about 1.5–2 cm in diameter covered by entire, brown prophylls. *Prophylls* 2–3 per stem, brown, innermost being longest, to 20 cm, entire or irregularly broken, rarely fibrous and forming a poorly developed reticulum at apex. *Basal leaf* linear, usually longer than the scape, 0.5–2.5 cm wide, flat or margins inrolled to some extent, rarely sub-terete. *Scape* erect, simple or bearing a few erect branches. *Bract leaves* 5–6 sheathing the stem, often overlapping, herbaceous with dry apex. *Inflorescence* several-flowered, inner spathe 8–14 cm, outer 2–3 cm shorter, apices dry. *Flowers* scented, yellow, with a large, deeper yellow nectar guide and a dark, brown to purple crescent on each style crest; *outer perianth segments* oblanceolate, to 5.5 cm long, limb to 3.5 cm long and 2 cm wide; *inner perianth segments* lanceolate to 4.5 cm long. *Filaments* to 1.3 cm long, joined in lower part; *anthers* 7–9 mm long. *Style* about 8 mm, branches about 1.5 cm long, to 8 mm broad, crests 1–1.3 cm long. *Ovary* about 1.5 cm long, clavate; *capsule* about 3 cm long. *Seeds* depressed, triangular. *Chromosome number* $2n = 12$, *Mauve s. n.* (PRE) (Fig. 3A).

Flowering time: Spring to early summer.

Distribution: Along watercourses, widespread in the eastern Cape, Lesotho, Natal and extreme south eastern Transvaal (Fig. 16).

Icones: Baker, Bot. Mag. *Tab. 6174.* 1875; Batten & Bokelmann, Wild Flowers of the Eastern Cape Province. *Pl. 34, fig. 5.* 1966; Obermeyer, Fl. Pl. Africa 40: *Tab. 1581.* 1970.

Moraea huttonii is, like most aquatic or semi-aquatic plants, very widespread. It can easily be identified by its habitat and by the conspicuous violet to brown marks on the style crests. In spite of its wide distribution and frequency, it remained poorly understood for many years. It was originally described by Baker as a species of *Dietes*, the cormous nature of the rootstock being misunderstood. In later works, Baker (1892, 1896) ignored the species altogether and included specimens of *M. huttonii* under *M. spathulata* (as *spathacea*) and *M. baurii*. N. E. Brown (1929) also included *M. huttonii* under *M. spathulata*. In 1969 Mrs. A. A. Mauve of the Botanical Research Institute revived Baker's species, transferring it, correctly, to *Moraea*.

Moraea rivularis Schl. must be included in *M. huttonii*, as there is no doubt it is the same species. *Moraea baurii* presents more of a problem. The type specimens are incomplete, lacking leaves or corms, and the flowers do not show the very typical violet mark on the style crests. The determination is based mainly on Baur's ecological note that the plants grow along streams. *Moraea baurii* is, therefore, only tentatively included as a synonym of *M. huttonii*.

27.30 (Vryheid): Oshoek, Wakkerstroom (-AC), *Mauve 4485* (PRE); *Devenish 89* (PRE); Donkerhoek, Utrecht district (-AD), *Devenish 1416* (PRE).
28.27 (Senekal): Ficksburg (-DD), *Fawkes 219* (NBG).
28.28 (Bethlehem): Leribe (-CC), *Dieterlen 354* (NH, PRE); *Dieterlen 7049* (GRA, SAM); Mont aux Sources (-DB), *Hutchinson, Forbes & Verdoorn 2* (NH, PRE); *Trauseld 264* (PRE); *Sidey 1995* (PRE).

28.29 (Harrismith): Near Cathedral Peak Hotel (-CC), *Schelpe 892* (NH, NU); Cathedral Peak area, *Dohse 132* (NH, PRE).
29.27 (Maseru): Mapotong (-BB), *Schmitz 1265* (ROML); Putsua mountains, Mafeteng district (-D), *Esterhuysen 13171* (BOL); Makhaleng (-DB), *Compton 21040* (NBG).
29.29 (Underberg): Giants Castle (-AB), *Skead 178* (NU); Giants Castle, Mumden stream, *Trauseld 998* (PRE); The Hook, Mooi River (-BD), *Bourquin 312* (NU); Ross, Umgeni Poort, *Moll 2666* (PRE); Fort Nottingham, *Mauve s. n.* (PRE 30478), *2426A* (PRE); Nottingham/Bulwer road (-DB), *Mauve 4472* (PRE).
29.30 (Pietermaritzburg): Lions River (-AC), *Moll 1180* (NU, PRE).
30.28 (Matatiele): Between Maclear and Naude's Nek (-C), *Werdermann & Oberdieck 1132* (PRE).
30.29 (Kokstad): Mieliefontein (-BC), *Strey 9161* (NH, PRE).
30.30 (Port Shepstone): Dumisa (-AD), *Rudatis 691* (LD).
31.28 (Umtata): Baziya (-CB), *Baur 514* (BOL).
32.26 (Fort Beaufort): Hogsback (-DB), *Bokelmann 5* (NBG).
32.27 (Stutterheim): Boma Pass, Keiskammahoek (-CA), *Acocks 9101* (PRE).
32.28 (Butterworth): Kentani (-CB), *Pegler 1206* (BOL).

EXCLUDED TAXA

1. **Moraea balenii** Stent, Fl. Pl. Africa *Tab. 301*. 1928.

The species figured with the type description is a small plant (stem 23 cm high) with a long conduplicate leaf and prophylls which break up into rigid bristles. It was described from a specimen cultivated at the National Herbarium, Pretoria, which flowered in June and was reported to have been found at high altitudes near Katberg, flowering in March.

A search for a plant matching this description at Katberg proved fruitless, but another very large conspicuous species of yellow flowered *Moraea* was found in this area (*M. reticulata*). This species has a stem 40–60 cm long, a canaliculate leaf, and characteristic prophylls and corm tunics which are fibrous, with the inner prophyll extending well above the ground as a reticulate sheath.

Moraea balenii itself bears no close resemblance to this *Moraea* and is actually very similar to a second species, *M. galpinii* which has a short stem, bristle-like prophylls and a leaf with inrolled margins. *Moraea galpinii* flowers in August and September in the wild. It seems possible that *M. galpinii* and a *Moraea* from Katberg became confused in cultivation. In view the of possibility of an error, *M. balenii* has been excluded and unless a plant matching the description can be found at the type locality, this species will remain one of doubtful validity.

2. **Moraea spathulata** var. **natalensis** Baker, Fl. Cap. 6: 14. 1896.

The specimens cited under this variety belong to several species including *Moraea ardesiaca*, *M. moggii*, *M. spathulata* subsp. *spathulata*. The diagnosis is too brief to make it possible to decide on which of the specimens it was based.

3. **Moraea trita** var. **foliata** N. E. Br., Trans Roy. Soc. S. Africa 17: 347. 1929.

The type of this taxon, which is at Kew Herbarium, is a Wilms collection (number *1418*) from Devils Knuckles and dated February 1888. The specimen is identical to the type of *Moraea trita* (= *M. stricta*), also at Kew (*Wilms 1419*, Lydenburg, September 1895).

Wilms material examined at Paris indicates a possible error. A specimen, *Wilms 1418*, also labelled Devils Knuckles, February 1888, is not the same as the Kew specimen with the same date and number. The Paris specimen is *Moraea elliottii*, a species flowering in summer and common in February in the area. *Moraea stricta*, typically leafless when flowering or with a dead, terete leaf adhering to the scape, flowers in spring. It seems that the Kew specimen named *M. trita* var. *foliata* is simply a collection of *M. stricta* with old, dead leaves adhering to the stem and that the herbarium ticket may have been placed with the wrong collection.

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A SYNOPSIS OF THE AFRICAN SPECIES OF *PANDANUS*[1]

BENJAMIN C. STONE[2]

The taxonomy of the African species of *Pandanus* is presently in a very unsatisfactory state. Since Warburg's monograph in 1900, a number of species have been described which have never been critically compared. The treatment by Warburg was itself very sketchy, as several species were founded on the poorest of specimens and unfortunately some have also been incorrectly, or inexactly, described. The earliest known African species was published by Palisot de Beauvois in 1804 (*Pandanus candelabrum*). Next described was *Heterostigma heudelotianus* Gaudich., 1843, now called *Pandanus heudelotianus* (Gaud.) Balf. f. In 1887, Henriques described *P. thomensis* from São-Thomé Island in the Gulf of Guinea; this was furnished with a particularly good description and figure. Rendle in 1894 in a paper entitled "Tropical African Screw Pines" attempted a complete review of the African species; he recognized eight species, five from West Africa and three from East Africa; of these, five were newly proposed species (*P. barterianus*, *P. welwitschii*, *P. rabaiensis*, *P. kirkii*, and *P. livingstonianus*). Up to this time, not much had been effected toward a subgeneric classification of the genus.

Warburg paid special attention to the African species of *Pandanus*. His monograph of 1900 includes 16 species credited to Africa, of which eight were species which he had described. Equally important was his attempt to establish a sound subgeneric, or rather sectional classification of the genus. The African species were arranged under Section *Keura*, *Vinsonia*, and *Sussea*. Sect. *Keura* is now correctly called *Pandanus*, since it includes the type species of the genus. Both *Vinsonia* and *Sussea* are names which Warburg took from the work of Gaudichaud, but these being invalid names (according to our present nomenclatural rules) effectively date only from Warburg's usage in 1900.

Since 1900, nine more species have been described. There are therefore at present 25 species to account for in any review of the African species. This does not include some *nomina nuda* and illegitimate names.

Martelli (1933) showed that one of the species described by Warburg and which he thought was from Africa, *Pandanus platycarpus* Warb., was wrongly localized; it proved to be from Java. This reduces the total to 24.

These 24 species are listed below according to the section of the genus to which they belong. After each is added a commentary on the present state of our knowledge of the species. Several names are reduced to the status of new synonyms.

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[1] Field work in East Africa and Madagascar and the Mascarene Islands during 1968 was supported by a Grant-in-Aid of Research from the Society of the Sigma Xi, U.S.A., which is gratefully acknowledged. I am grateful also to Dr. J. B. Gillett, of the East African Herbarium, Nairobi, and Dr. B. J. Harris, of the University College of Dar-es-Salaam, for their kind assistance.

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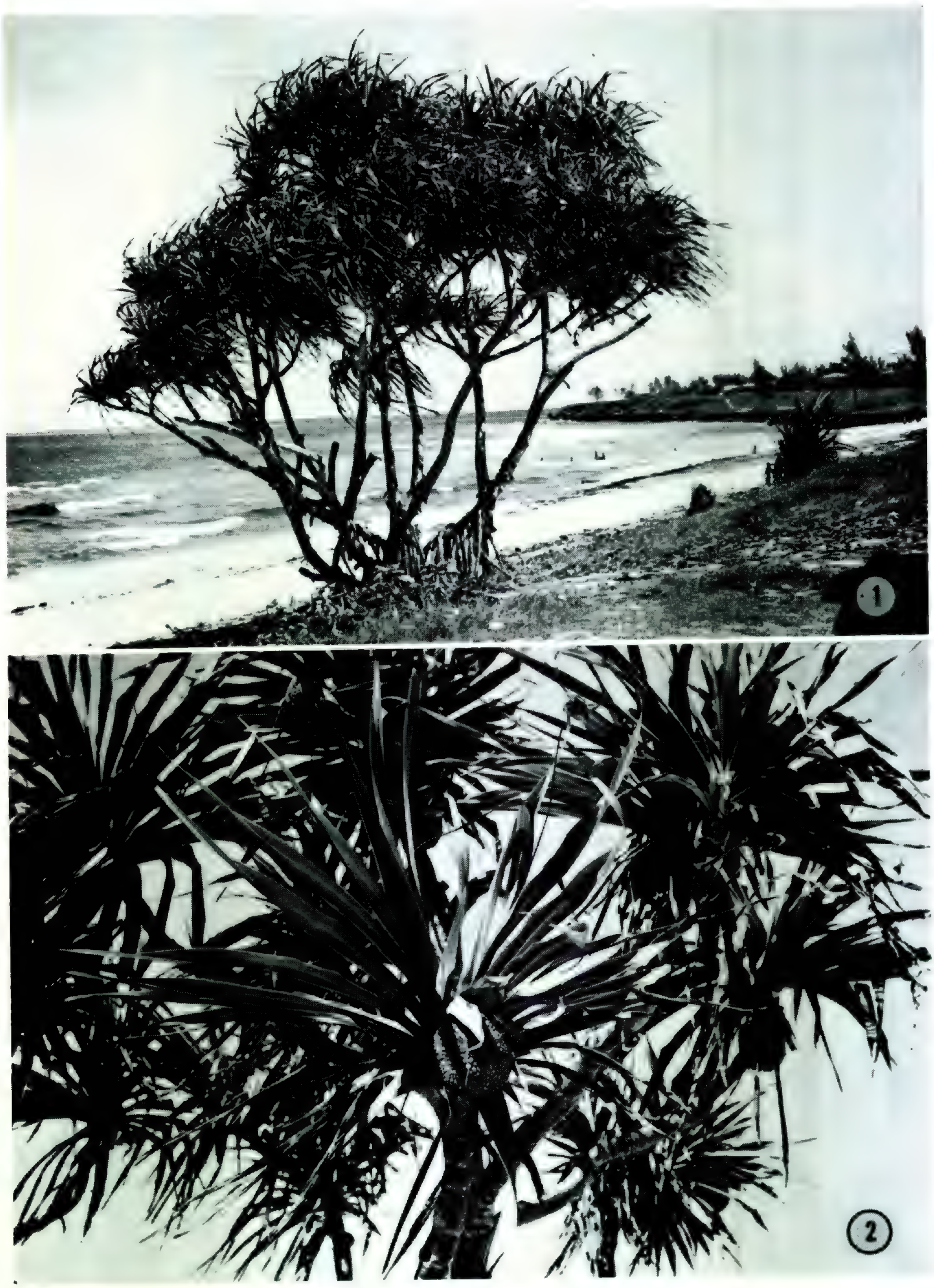
ANN. MISSOURI BOT. GARD. 60: 260–272. 1973.



FIGURES 1–2. *Pandanus kirkii* Rendle, at Oyster Bay, Dar-es-Salaam, Tanzania.—1. Adult trees.—2. Pistillate tree with immature head of fruit.

SECT. PANDANUS

Type species: *P. odoratissimus* L. f.
Type locality: Ceylon.
Syn. Sect. *Keura* (Forssk.) Kurz.

(1) *Pandanus kirkii* Rendle, Jour. Bot. 32: 326. 1894.—FIGS. 1–6.

Wright, in Thiselton-Dyer, Fl. Trop. Afr. CXLVIII Ord., 127.
TYPE: "Mainland opposite Zanzibar, Dr. Kirk, 1867 (Mus. Kew)."

P. heddei Warb., Pflanzenr. 3. IV. 9: 46. 1900. *Syn. nov.*
TYPE: *Hedde 31*, Dar-es-Salaam, beach.

P. usaramensis Martelli, Webbia 4: 415. 1914. *Syn. nov.*
TYPE: *Stuhlmann*, 1905, Dar-es-Salaam.

P. warburgii Martelli, Webbia 4: 36, *t.* 37, *fig.* 4–6. 1914; (*P. kirkii* Warb. *non* Rendle). *Syn. nov.*
TYPE: *Holtz*, East Africa.

Since Martelli has concluded that *Pandanus platycarpus* Warb. is not from Zanzibar as stated by Warburg (who gives E. H. L. Krauss as the collector) but is rather from Java, this can be omitted from synonymy.

Pandanus maximus Martelli, from Comoro, is probably but a large-fruited variety of *P. kirkii*.

Pandanus kirkii includes a number of minor forms, principally differing in the morphology of the phalanges, but in ways which are known to be quite standard and essentially meaningless from a taxonomic standpoint. The proportions of the phalanges, their differing dimensions, the depth of the sinuses between carpel tips, number of carpels per phalange, *etc.*, are all characters the variation of which has been demonstrated (Stone, 1967*b*) to occur in *P. odoratissimus* in a quite parallel way, without taxonomic import. This species probably occurs interruptedly all along the tropical East African coast wherever there is sandy beach habitat.

"Mainland opposite Zanzibar, 1867, Dr. Kirk" (K, holotype). [Note: Dr. Kirk was a companion of Livingstone on some of his African explorations.] KENYA: Kwale District, Twiga, 14 mi. S of Mombasa, tree 15 ft., no stilts, above high tide mark, with *Hyphaene*, *Salvadora*, *Pemphis*, *Ehretia*, *Cocos*, etc. *Verdcourt 3287* (EAH). —Kwale Districts, K7, N & S, Jadini, sealevel, tree 25 ft., with stilts, leaves ensiform just over 3 ft. long, peduncle to 1 ft. long, phalanges 6–11-celled, green becoming yellow-brown, together with *Casuarina* and *Guettarda speciosa* and *Sideroxylon inerme*, on sand just above high water-mark, *Greenway 9642* (EAH), pistillate and staminate. ZANZIBAR: Muaka, sealevel, *Vaughan 2308* (EAH), staminate. Mkadi Kis, "common all round the coast and on Pemba Isl." sand or coral rock, Mangapwani, *Greenway 1138* (EAH), staminate. TANZANIA: Tanga District, Kogome beach, 7 mi. NE of Pangani; coastal forest; near high-water mark in sandy areas on fringe of thick low shrubby cover; branched tree 15 m, bark smooth, dark gray; leaves glaucous; heads solitary, green; 5–9-celled drupes; *Drummond & Hemsley 3245* (EAH). [This specimen bore an unpublished name based on the adjective "cuneate" annotated by H. St. John.] Dar-es-Salaam, sealevel, *Leippert 5501* (EAH), staminate infl. only. Dar-es-Salaam, Oyster Bay, *Stone 7731*, *7732*, *7733*, *7734* (all KLU). 6 mi. SE of Bagamoyo Mbagani, HWM, *Harris & Gardiner 2559* (KLU).

These specimens are only moderately variable, and there seems no difficulty in considering them all to represent *Pandanus kirkii*. The leaves reach 127 cm long and 4.7–6.6 cm wide. The marginal teeth near the base range from 1–3 mm long. The male inflorescences showed about 13 spikes up to 7 × 2.5 cm. Leaf characters varied over a very narrow range. Phalanges differed considerably but

FIGURES 3–4. *Pandanus kirkii* Rendle; Oyster Bay, Dar-es-Salaam.—3. Juvenile plant.—4. Adult tree; base of trunk, showing proproots.

mainly in absolute dimensions (the largest ones about twice the size of the smallest) and in the depth of the sinuses separating the carpel tips, these reaching a depth of 7–8 mm or even more. Carpel number remained quite steady (generally, 5–11; mean at 9).

As the collectors' notes verify, this is typically a plant of sandy beaches just above high-water mark. Also "coral rock" is mentioned as a habitat. The plant associates are characteristic sandy-beach species.

Rendle's original description of this species was very brief; he noted however a similarity to *Pandanus odoratissimus*. In this he was certainly correct. This similarity is so marked that I do not feel it is necessary to provide an extended description. Instead it seems sufficient to refer to the very complete description which I have supplied earlier for *Pandanus odoratissimus* L. f., *sensu lato* (Stone, 1967*b*), and to single out the points of difference between that and the present species.

Pandanus kirkii: marginal teeth of leaves, near the base, relatively short, rarely over 2–2.5 mm long, greenish-white to white. Ripe phalanges with weakly developed shoulders, or none (see Fig. 6); pericarp yellow-orange.

Pandanus odoratissimus: marginal teeth of leaves, near the base relatively long, usually at least 4–6 mm and sometimes to 8–11 mm long,

FIGURES 5–6. *Pandanus kirkii* Rendle; Oyster Bay, Dar-es-Salaam.—5. Staminate inflorescence. (*Stone 7731.*)—6. Phalanges (fully ripe); black disc (lenscap) is 5 cm wide. (*Stone 7732.*)

white. Ripe phalanges with strongly developed shoulders (Stone, 1967*b*, Fig. 4, 6), red, dark red, or vermilion.

As I have pointed out (Stone, 1967*a*) the carpels forming a phalange are variable in number, and although previously much taxonomic weight was placed on this feature, it is not now considered entirely dependable. With reference to normal carpel, number, this is in *Pandanus kirkii* apparently somewhat higher than in *P. odoratissimus*. Rendle in his original description states that *P. kirkii* has phalanges of 7–9 carpels; Warburg (1900) modifies this to 8–14 (and also states "Zanzibar" as the locality, while Rendle clearly specifies "mainland opposite Zanzibar."). For his *P. heddei*, Warburg does not give carpel number, though in the key it comes after the heading "Drupae multiloculares." Martelli's illustration of this species (1914: *tav. XI, fig. 8*) shows a phalange with 6 carpels. His illustration of *P. usaramensis* Martelli (1914: *tav. XIII, fig. 4*) shows a phalange of 10 carpels. *Pandanus warburgii* Martelli is "*P. kirkii* Warb. *non* Rendle," and the type is presumably the "Zanzibar" specimen noted by Warburg as having 8–14 carpels per phalange. As for *Pandanus maximus* Martelli, the phalange illustrated by Martelli (1914: *tav. XI, fig. 2*) is 12-carpellate, but it is moreover rather larger than any specimens of African *P. kirkii* which I have seen.

It is hoped that the liberal inclusion of illustrations here will add to ease of identification of *Pandanus kirkii* (Figs. 1–6).

Probably the most interesting outcome of this study of *Pandanus kirkii* is that it proves to differ constantly from *P. odoratissimus* in a few, apparently rather trivial, characters, but at the same time approaches more closely the characters of the Pacific Island species *P. tectorius* Parkinson[3] and its immediate allies.

It is not at present possible to discuss in detail the comparable features of *Pandanus kirkii* and *P. tectorius*. By emphasizing their similarity in contrast to *P. odoratissimus* I wish merely to show that these three taxa (which have been split up into many finer components by Martelli, Warburg, and St. John) whether or not it is agreed that they are species or "superspecies" or something in between, occupy three distinct regions within which great internal variation occurs that is in my opinion of little taxonomic importance and display a few constant characters. The length and color of the leaf-margin teeth, the color of the ripe fruit pericarp, and the development (or lack of same) of the phalange shoulders, are these relatively constant features. Certainly they assort into three groups; and the distinction between *P. odoratissimus*, and the other two, is more obvious than that between *P. kirkii* and *P. tectorius*. In some ways it may be said that *P. kirkii* is intermediate between the others; in some other ways, it is very much more like *P. tectorius* than like *P. odoratissimus*. Difficulties arise to prevent much more cogent discussion, chiefly the great, and difficult, variation of the Pacific Island forms. As I have already stated, even if we accepted the name *P. tectorius* (by providing a neotype from the classic locality, Tahiti) this does not mean acceptance of either a narrow or a broad species concept. That Martelli could

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[3] *Pandanus tectorius* is a controversial name that requires neotypification, if it is to be used at all with any precision. I imply a Tahitian form.

describe seven species from Tahiti alone (without mentioning *P. tectorius*!) and many others from Polynesian Islands; yet also treated *P. tectorius* as a complex species having many varieties (in such places as the Philippines, Borneo, Java, and New Caledonia), and even seemed to think that the "pure" form (with no varietal epithet) occurred on Rodriguez Island (Mascarenes), shows clearly the importance of the problems that arise in attempting comparisons.

Despite these thorny problems it is worthwhile to emphasize the evidently stronger differences between *Pandanus kirkii* and *P. odoratissimus*, because of their bearing on geographical relationships. That is to say, the available evidence shows three (at least) mainly non-overlapping areas of distribution associated with the character-complexes ("species") described. These are, first: Coasts of India (Bombay and south, then north to Bengal); Maldives; Ceylon; coasts of Burma, Thailand, Malaya, East Sumatra, "Indo-China," Hong-kong, Borneo, Philippines (especially the western side), Celebes. This area is the "home" of *P. odoratissimus*. (I have reason also to include Taiwan and at least the South Ryukyu Islands). The second area: The entire tropical coast of East Africa; probably also Comoro Islands (? *P. maximus*); probably Seychelles (*P. balfourii*); possibly Rodriguez. This is the area of *P. kirkii* and its immediate relatives. The third area: The Eastern Pacific; Melanesia; probably North Queensland; Sunda Islands west to Java (and probable slight overlap with the first area). This is the area of *P. tectorius* and its relatives. How many species are involved it is too early to tell. (*P. boninensis* hardly can be distinguished from *P. fragrans* Gaud. of the Marianas; some Hawaiian and Tahitian forms look extraordinarily similar; *etc.*) On the basis of these areas we can discriminate two reasonably homogeneous taxa, *P. kirkii* and *P. odoratissimus*, which I think can fairly be treated as species, and which occupy the first two areas mentioned. The remaining area contains, very probably, more than one species of this immediate relationship (*P. tectorius*, *P. fragrans*, and *P. pedunculatus* R. Br. are among those which appear to have the best claims to rank as species), and certainly a large number of minor taxa (some so minor as cultivars). Significantly, it is this latter area which includes forms that most closely resemble *Pandanus kirkii*. There may however be a "cline" evident between *P. odoratissimus* in Ceylon, through the Maldive and Laccadive Atoll populations, to *P. kirkii*. One difficulty here is that *P. odoratissimus* is a cultivated plant. As will be seen below, it is definitely known from Zanzibar. The possibility of hybridization must be kept in mind; yet it does not seem very much in evidence.

(2) *Pandanus odoratissimus* L. f., Suppl. 424. 1781.

TYPE: Ceylon, *Thunberg*.

ZANZIBAR: Pemba Island, Mtambele Gai Lamtungi, 14 mi. S of Chakechake, in wet meadow-groves; cultivated trees to 8 m × 10 cm; lvs. glaucous beneath; spines of basal margins 6 mm long; those of midrib retrorse. *St. John 26611* (EAH), staminate. "Flowers worn as garlands by women."

Quite typical of the species is this specimen from Pemba. It is cultivated partly for the leaves, partly for the fragrant male inflorescences. Use of the plant is widespread in India, Ceylon, Malaysia, *etc.*, but this is the first unambiguous record from Africa.

The plants may easily be distinguished from *Pandanus kirkii* by the much longer and very white leaf spines. The phalanges differ in being dark red, with very markedly developed shoulders. It is generally the male plants, however, which are in cultivation; the female may well be absent from Pemba.

Sect. Dauphinensia

St. John, Pacif. Sci. 14: 228. 1960.

Type species: *P. dauphinensis* Martelli (Madagascar).
Type locality: Ft. Dauphin, S. Madagascar.
Syn. "*Dorystigma*" Gaud. (*nom. illeg.*); *Doornia* De Vriese; both as genera.

The species of this section are found in the Mascarene Islands, Madagascar, and Africa. All of them, not only the African species, are in a state of more or less confusion. The species early described were very briefly characterized; in several cases the original specimens are inadequate or they have been lost or destroyed. Later species, even if well described, have hardly been critically compared to the older species. This appalling state of ambiguity still shrouds our knowledge of this section in Africa. On the other hand, it is a very clear-cut section, and can easily be distinguished from the other sections present in Africa. From sect. *Pandanus*, the present section differs in having the pistillate inflorescence compound of several (as many as 13) cephalia spicately or racemosely arranged on a long, stout peduncle. The phalanges differ in having flat tops, the stigmas small, sessile, and reniform-rounded, arranged around the edge of (or rarely slightly within) a central, polygonal, slightly depressed areola. The individual carpels, in other words, present no individuality except as (1) stigmas, externally; and (2) seed-containing locules, internally.

(1) *Pandanus rabaiensis* Rendle, Jour. Bot. 32: 325. 1894; Jour. Linn. Soc. Bot. 30: 432, *t. 34., figs. 1–6.* 1895.—Fig. 7.

TYPE: "Rabai Hills, Mombasa, W. E. Taylor, 1886 (Herb. Mus. Brit.)."

P. stuhlmanni Warb., Pflanzenr. 3. IV. 9: 57. 1900. *Syn. nov.*

Rendle's original description of this was so brief that Warburg (1900) considered it "incertae sedis" (Warburg apparently seldom if ever used specimens from other herbaria on loan for study, a major drawback in his work). Rendle had first said: "*P. Rabaiensis* Rendle in Journ. Linn. Soc. ined. A species with the stamens spicately arranged in the stalked male flowers; and fruits somewhat resembling those of the Malagasy *P. utilis* Bory but with a shorter, more rounded top." This description (which was followed by a more complete one in Jour. Linn. Soc. Bot. 30: 432. 1895), though it legalizes the name, conveys no idea in the least of the plant it is supposed to portray; yet it is the only description seen (apparently) by Warburg, who merely translates this into Latin: "Drupae *P. utili* paullo similia, sed apice breviore et magis rotundato." Truly a case of the blind leading the blind! In the Herbarium of the British Museum (Natural History) there is still preserved the type of *P. rabaiensis*. It is provided with several sketches and notes by Rendle. A study of this specimen clearly shows that it is a species of sect. *Dauphinensia* and further suggests that Warburg's *P. stuhlmannii* is the same. Drawings of the phalanges, both pistillate and staminate,

FIGURES 7–8.—*Pandanus rabaiensis* Rendle. Dar-es-Salaam, coll. 1909. (Specimen in FI.) Fruiting spadix.—8. *Pandanus goetzei* Warb. Fruiting spadix. (*Greenway 4192.*)

are attached to the sheets; these are clearly the basis of Martelli's published illustrations (1914: *tav. 23*). It is not possible to verify whether the staminate material is truly conspecific; the fruits must be selected as the proper lectotype material.

Pandanus goetzei Warb. is very similar. Warburg differentiates it from *P. stuhlmannii* by the shape of the cephalia (ovate rather than oblong) and the larger drupes (4 cm *versus* 3 cm). The type is destroyed, but a photo in the Martelli Herbarium (FI) shows a peduncle with 4 ovoid cephalia, according to Warburg's description 10–12 × 8–10 cm. Warburg states "syncarpia compluria" which may mean that there may have been more than 4; indeed the photo suggests that one (a terminal one) may be lacking. I have seen no authentic material of *P. stuhlmanii*. In the East African Herbarium (Nairobi) there are some specimens identified as *P. stuhlmannii* and some as *P. goetzei*. One of them (*Greenway 2584*) bears the determination *P. goetzei* and the signature, Max Burret. Burret probably identified a duplicate in the Berlin Herbarium before World War II, and it seems plausible that he was able to compare it with Warburg's type specimen. It is from Zanzibar (Yozani, in swamp forest). I think, however, that it is *P. rabaiensis*. Another specimen in EAH, *Greenway 5380*, is certainly the same species; it is from Mafia Island, Tanganyika, at 20 feet altitude. The specimens in EAH annotated as *P. stuhlmannii* are generally from higher altitudes; *Drummond & Hemsley 1420* is from the Eastern Usambara hills, at 1100 m; other

specimens are from approximately the same locality ("Amani"). One specimen from this area is determined as *P. goetzei* (*St. John 26602*). It seems very difficult to believe that these are specimens which pertain to more than one species, and I consider that they are *P. goetzei.*

In the Martelli Herbarium (FI) there is a fruiting spadix without indication of collector; the label says "*Pandanus rabaiensis*; Dar-es-Salaam, 1909." This has noticeably oblong cephalia, and they are more numerous on the spadix, probably 8 or 9 in all. This corresponds reasonably well with the type of *P. rabaiensis.*

If there are really two species, one with fewer, ovoid cephalia; the other with more numerous, oblong, cephalia, then the probable correct names for these seem to be *P. goetzei* Warb. for the former, and *P. rabaiensis* Rendle (syn. *P. stuhlmannii* Warb.) for the latter. It is also possible that the former is principally found in upper altitudes (*e. g.* 1000 m) while the latter is essentially of the lowlands, and not far from the coast. However, all these distinctions are of rather dubious value. It is simply impossible at present to decide how many species are represented, but it seems very probable that one, or possibly two, species are involved; surely not three.

In the key to *Pandanus* by Dale and Greenway (in their book *Kenya Trees and Shrubs*, 1961) two species are included, *P. kirkii* and *P. rabaiensis.* Of the latter they say: "Tree usually associated with fresh or brackish water; drupes 1–5–celled, 1.5″ long." Brenan and Greenway, in "Checklist of the Forest Trees and Shrubs of the British Empire, no. 5" list both *P. stuhlmannii* Warb. and *P. goetzei* Warb. but omit *P. rabaiensis.*

TANZANIA: Mafia Island, in *Philippia mafiensis* formation, wet valley bottoms, Utmaini-Miwani, *Greenway 5380* (EAH). Zanzibar, Yozani, *Greenway 2584, 1302*; *Vaughan 2287* (all EAH).

(2) *Pandanus goetzei* Warb., Bot. Jahrb. Syst. 33: 350. 1900; Planzenr. 3. IV. 9: 57. 1900.—FIG. 8.

TYPE: "German East Africa, Uhehe, Lofio River" (*Goetz*).

KENYA: E. Usambara, Bomole Hill, Amani; 1100 m, *Drummond & Hemsley 1420* (EAH); *Greenway 4192* (EAH); *St. John 26602* (EAH).

(3) *Pandanus engleri* Warb., Bot. Jahrb. Syst. 34: 151. 1904.

TYPE: Tanzania, Usambara W., "schluchten unterhalb Sakare, 800 m." Engler, Reise nach Ostafrik. no. 981. Sept. 1902.

Warburg says "very close to *P. goetzei* from Uhehe." He describes the cephalia as oblong and the drupes as 3–5-celled. It seems very dubiously distinct.

Martelli gives no illustration. The type collection perhaps is destroyed, but many of the Berlin monocots were saved. Fresh collections from the type locality would be necessary to establish the identity of this species. Very likely, it will prove to be a synonym of *Pandanus goetzei.*

SECT. VINSONIA

Warb. Pflanzenr. 3. IV. 9: 44. 1900, *pro parte*

Type species: *Pandanus utilis* Bory.
Type locality: Mascarene Islands or Madagascar.

(1) *Pandanus utilis* Bory, Voy. 2: 3. 1804.

TYPE: Madagascar, *Bory*; or Reunion?
TANZANIA: Amani, cult. in plantation BH-7; to 30 ft. Tall, *Greenway 1714* (EAH). Leaf spines red.

In Africa, found in cultivation only.

The stiffly erect very glaucous leaves, with red marginal spines, the solitary pendulous oblate cephalium with green-and-orange phalanges all quickly identify this species.

(2) *Pandanus thomensis* Henriques, Soc. Brot. Bol. 5: 206, *pl. E.* 1887.

TYPE: São Thomé Isl., Gulf of Guinea. "Regio inferior usque 500 m (Moller); ins. Rollas (F. Quintas)."

A well-characterized species.

The closest relative seems to be the very recently described *P. mayotteensis* St. John, from Mayotte Island in the Comoro group.

DOUBTFUL SPECIES

Pandanus hahnii Warb. Pflanzenr. 3. IV. 9: 56. 1900.

TYPE: Martinique, *Hahn*, in cultivation.

Derivation dubious: East African Islands?

The species of sect. *Vinsonia* are well-marked and few. There should be no difficulty in identifying these in Africa.

SECT. HETEROSTIGMA
(Gaudichaud, as genus, Atl. Bot. Voy. Bonite, *t.* 25. 1843)
B. C. Stone, *stat. nov.*

Type species: *Pandanus heudelotianus* (Gaud.) Balf. f., Jour. Linn. Soc. 17: 49. 1879.
Type locality: Senegambia, *Heudelot*. Near Dakar.

The following species were included in sect. *Sussea* by Warburg, Martelli, and other authors, or were not assigned to sections. *Heterostigma* Gaud. has been resuscitated at sectional rank for a group of species found in Africa and Madagascar.

The classification of this section is in a pitiful state. Virtually none of the species in Africa are represented by adequate specimens. The original descriptions are generally far below the standard required for clarity and comprehensibility. Once again, though, as was the case in sect. *Dauphinensia*, the species remain in a sort of impenetrable miasma, yet the section itself is very well-characterized and easy to distinguish both in the field and in the herbarium, especially the former.

Vast difference exists between C. H. Wright's treatment of the African *Pandanus* (in Thiselton-Dyer, Fl. Trop. Afr. Order CXLVIII, pp. 127 *et. seq.*) and Hutchinson's treatment in Hutchinson & Dalziel, *Flora of West Tropical Africa* (fam. 176, p. 392, and *fig. 318*). Wright accepts 16 species (of course for both East and West Tropical Africa); while Hutchinson accepts one species, *viz. P. candelabrum* Beauv., under which he includes *P. heudelotianus*, *P.*

kamerunensis, *P. barterianus*, *P. leonensis* Hort., *P. unwinii*, and suggests that the following should also be included: *P. togoensis* and *P. kerstingii*. Of these, Wright accepted the first three as distinct and *P. candelabrum* as further distinct; the remainder he does not mention, several having later dates. *Pandanus leonensis* Hort. is in any case a doubtful horticultural plant and only a *nomen nudum*. Nevertheless, this should demonstrate a considerable difference in opinion. According to Hutchinson's notes, he had available about a dozen more specimens to study than did Wright.

Under these circumstances I can do no more than list the names which at least will group them properly in one section. W = Africa, E = East Africa.

(1) *Pandanus heudelotianus* (Gaud.) Balf. f., Jour. Linn. Soc. Bot. 17: 49. 1879.
(W) *Heterostigma heudelotianum* Gaud., Bot. Voy. Bonite *t. 25, fig. 15–31*. 1843.
TYPE: Senegambia, *Heudelot*, in upper Guinea, [= Nigeria].

(2) *Pandanus candelabrum* Beauv., Fl. Benin & Oware 1: 37, *t. 21–22*. 1804.
(W) *Tuckeya candelabrum* (Beauv.) Gaud., Bot. Voy. Bonite *t. 26, fig. 10–20*. 1843.
TYPE: Benin, West Africa, "Banks of the River Formosa, near Agathon" (*Beauvois*), = Nigeria.

(3) *Pandanus kamerunensis* Warb., Pflanzenr. 3. IV. 9: 66. 1900.
(W) TYPE: Cameroons, *Schran*.

(4) *Pandanus barterianus* Rendle, Jour. Bot. 32: 324. 1894.
(W) TYPE: Fernando Po, *Barter 2*.

(5) *Pandanus welwitschii* Rendle, Jour. Bot. 32: 324, *t. 347*. 1894.
(W) TYPE: Angola, Pungo Andongo, banks of Cuanza R. nr. Candumba and Ilha Calemba, *Welwitsch 5770, 1015*.

(6) *Pandanus livingstonianus* Rendle, Jour. Bot. 32: 326. 1894.
(E) TYPE: Mozambique, Delta of the Zambesi R., mouth of Luabo R., *Kirk*.

(7) *Pandanus petersii* Warb., Pflanzenr. 3. IV. 9: 66, *fig. 17: J–L*. 1900.
(E) TYPE: Mozambique, on banks of Lucuare and Munanche Rivers, *Peters*.

(8) *Pandanus teuszii* Warb., Pflanzenr. 3. IV. 9: 67. 1900.
(W) TYPE: Gaboon, *Teusz*.

(9) *Pandanus chiliocarpus* Stapf, Jour. Linn. Soc. Bot. 37: 530. 1906.
(C.E.) TYPE: Uganda, Toro, by the Usonei and Durra Rivers, *Dawe 523*.

(10) *Pandanus umbellatus* Martelli, Webbia 4: 435. 1914.
(W) TYPE: Ivory Coast, Guinea, *Jolly 32* (staminate). This may be the male of *P. candelabrum*.

(11) *Pandanus togoensis* Warb., Notizbl. Bot. Gart. Berl.-Dahlem App. 22: 43. 1909.
(W) TYPE: Togoland, W. Trop. Afr.
This species was omitted in Martelli's listing (1913).

(12) *Pandanus unwinii* Martelli, Webbia 2: 434. 1908.
(W) TYPE: South Nigeria, near Benin, *A. H. Unwin*, Sept. 1907 (FI).
Reduced to *P. candelabrum* by Hutchinson, I believe correctly.

INCERTAE SEDIS

(1) *Pandanus hemiacanthus* Peter, Fedde Rep. Sp. Nov. Beih. 40(1): 100, 111. 1929.
TYPE: Tanzania.
(2) *Pandanus kerstingii* Warb. Notizbl. Bot. Gart. Berl. App. 22: 3, 43. 1909.
TYPE: West Tropical Africa.
Misspelled by Martelli ("Kerstingerii").

NOMINA NUDA

(1) *Pandanus sessilis* Bojer, Hort. Maurit. 302. 1837. Pemba Isl. (nr. Zanzibar).
(2) *Pandanus leonensis* Hort. *ex* Wendl. Ind. Palm 46. 1854. Guinea.

NOMEN SUBNUDUM

(3) *Pandanus butayei* De Wildeman, Rev. cultures Coloniales 10: 15. 1902.
Lower Belgian Congo, N'Lemfu. R. P. Butaye, *Gillet 2250.*

This has a rather diffuse description which is probably legitimate and suggests that the plant is a "Sussea," which probably means it belongs in sect. *Heterostigma.*

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POLLEN MORPHOLOGY AND RELATIONSHIPS OF THE FLACOURTIACEAE[1]

Richard C. Keating[2]

Abstract

Light microscopic studies of the pollen of 51 genera and 151 species of Flacourtiaceae were made from KOH-acetolyzed specimens. The pollen is always found as single grains and is usually triaperturate with compound apertures, isopolar, and psilate to reticulate. Within the triaperturate type, the pollen of the family ranges from unspecialized to moderately specialized. Differences in pollen morphology do not often serve to delineate the taxonomic tribes. The Berberidopsideae and Oncobeae show a considerable range of size and sculpturing patterns. Scolopieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. Pollen of Casearieae is similar to that of the preceding group of tribes but adds more specialized trends. Both Pangieae and Paropsieae are isolated in the family, and the Paropsieae should be assigned to the Passifloraceae. Comparisons with families of putatively related orders indicate that the relationships of the Flacourtiaceae based on pollen morphology accord well with Takhtajan's system.

By one recent estimate (Hutchinson, 1967), the Flacourtiaceae include about 90 genera and 1284 species. This large, tropical family has received little attention by taxonomists and morphologists in proportion to its size and evolutionary importance. Such neglect seems to be due to the complex taxonomic history of the family and its reputation as a taxon in which to place many genera of uncertain status (*cf.* Williams, 1965). As understood by Warburg (1893) and Gilg (1925) the family is quite heterogeneous and indeterminate. The concept of the family has been greatly improved by the generic treatment of Hutchinson (1967).

The Flacourtiaceae include some very primitive genera in the tribes Berberidopsideae and Oncobeae (Hutchinson, 1967), and the family usually occupies a basal position in the Violales (Cronquist, 1968; Takhtajan, 1969), Cistales (Gundersen, 1950; Thorne, 1968) or Bixales (Hutchinson, 1959). In most of these schemes the Violales are considered close to the Theales, but their relationship to Ranalian lineage is still controversial (Takhtajan, 1969; Meeuse, 1970). A brief resumé of suggested affinities has been presented by Angely (1966). As many as nine orders have been suggested to be derived from flacourtiaceous stock (Takhtajan, 1969), and many of these suggestions will probably prove correct. However, in spite of the potential importance of microscopic characters in interpreting evolutionary trends, such observations are so scarce in many families as to make many statements of taxonomic affinity with Flacourtiaceae fall within the realm of speculation. Recognizing that pollen provides only one line of evidence in phylogenetic studies (Thorne, 1963), I have begun with a survey of the light microscopic features of the pollen in order to provide an

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[1] I am grateful to the curators of the U. S. National Herbarium and of the Missouri Botanical Garden for permission to use the collections and for their assistance. The SEM photomicrographs (Figs. 171–172) were made possible through the courtesy of Walter H. Lewis, to whom thanks are extended.

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Ann. Missouri Bot. Gard. 60: 273–305. 1973.

overview of the family. The value of this feature for comparative investigations has been attested to by many (*cf.* Canright, 1963). More intensive studies of the tribes will include studies of the wall morphology by scanning and transmission electron microscopy of which the present study will provide a basic reference. More detailed studies will definitely be needed to determine the trends of specialization of the wall structure and to better document relationships to other families.

Erdtman (1952, 1969) has called the Flacourtiaceae a eurypalynous family. When considered as understood by Hutchinson (1967) there is diverse pollen morphology, although several of the tribes show a monotonous uniformity. There is less diversity than in the more specialized families of the Malvales and Theales.

In his pollen study of the Alangiaceae, Reitsma (1970*b*) states that the work would not have been possible without reference to the recent monograph of the family. One of the formidable problems in my study was the need to sample herbarium specimens which were not well annotated. Large gaps in the monographic work on the family made the choice of specimens difficult. In order to prevent future confusion, vouchers from each specimen examined are listed by genus.

Previous treatments of flacourtiaceous pollen grains are not common. Erdtman's (1952) study of 25 genera and 35 species included genera which are not presently assigned to the family. Spirlet (1965) and Presting (1965) treated the tribe Paropsieae which has been placed in either the Flacourtiaceae or the Passifloraceae. Rethoré (1963) described pollen of *Tissonia*, *Sabourea*, and *Casearia* of Madagascar. Van Campo *et al.* (1965) and Bronckers (1967) have described pollen of six genera of Flacourtiaceae in their series on African palynology.

Materials and Methods

In the present study, 51 genera and 151 species of flacourtiaceous pollen have been examined. Due to their rarity, the three genera included in the tribes Alzateeae and Bembicieae are not represented. A number of pollen slides of putatively related genera, especially of Passifloraceae and Tiliaceae, were also prepared or were available for comparison. It has been noted that although the whole ecological amplitude of collections is needed to give a complete picture of pollen morphology, a good picture of a family can also be gained by an extensive rather than an intensive view (Whitehead, 1963).

The material was prepared by KOH-acetolysis (Faegri & Iversen, 1964). This gave clean preparations, and no damage to the exines was observed when compared to acetolysis alone. Expansion is negligible after this treatment (Reitsma, 1969). Pollen was mounted in glycerine-jelly with or without safranin-O added. Several authors have commented on the efficacy of measurements made from treated grains (Dickison, 1967). However, there appears to be no reason why the size and shape of KOH-acetylyzed, glycerine-jelly mounted grains cannot be considered characters in their own right. These methods are widely enough used to preserve the comparative value of such measurements. Whitehead (1965) calculated the conversion factor for pollen mounted in glycerine jelly when compared to silicone oil mounts. Measurements from glycerine-jelly mounts should be divided by 1.06 when compared to silicone-oil preparations.

Measurements of polar (P) and equatorial (E) dimensions were made of at least 20 grains per specimen.

Descriptions and Terminology

Descriptive terminology, already overproduced, is further confused by the addition of terminology from electron microscopy. It is important to avoid

confusing appearance with structure. Since most of the recent progress in recognition of wall layers has originated with electron microscopy, one should not use EM inspired terms for optical microscope observations where the structures cannot be clearly seen.

The terminology used here is based on Faegri and Iversen (1964) with some modifications as suggested by Erdtman (1952), Reitsma (1970*a*), Van Campo (1958), and Wittman and Walker (1965).

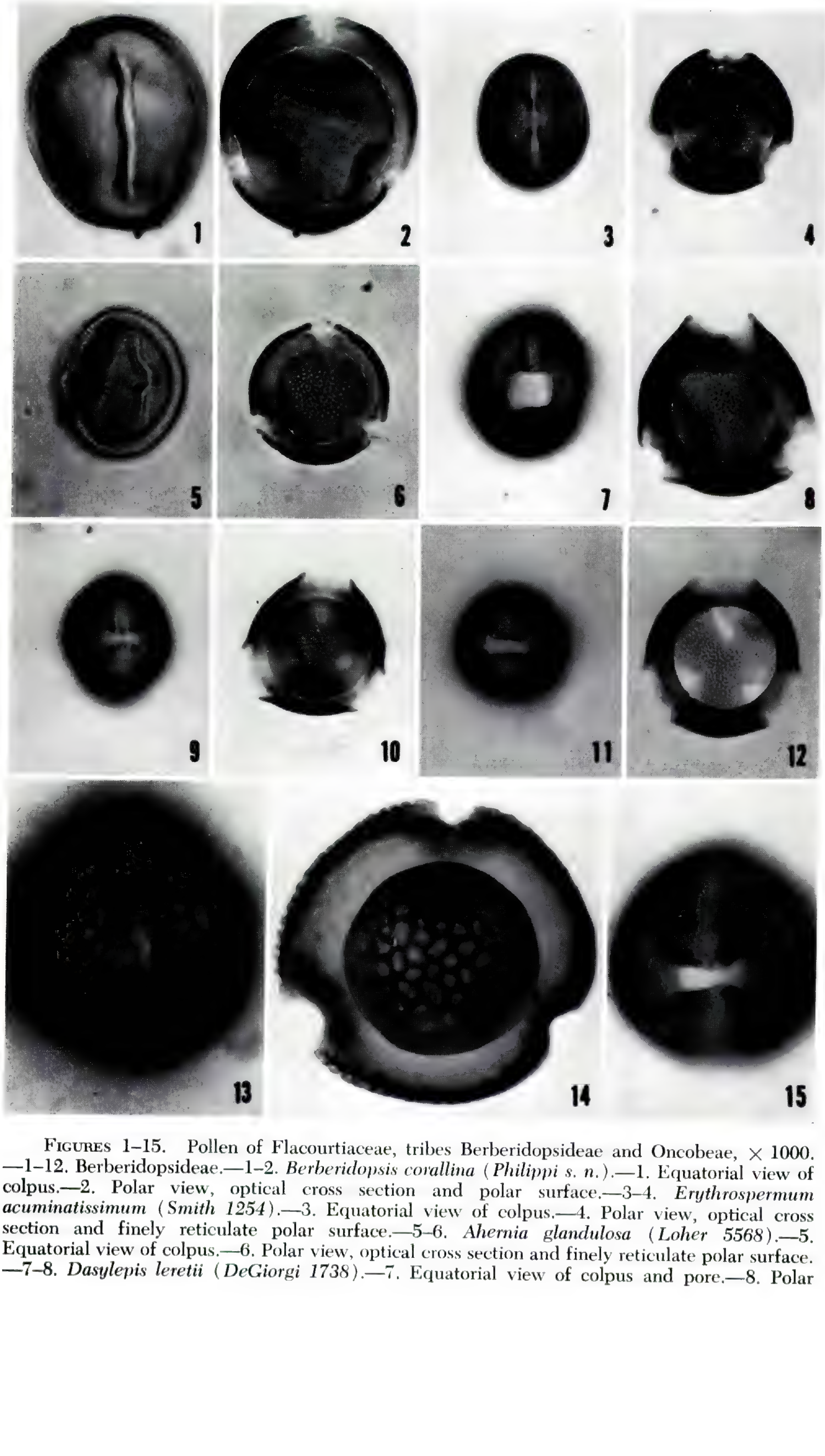
Grains of Flacourtiaceae observed in this study were always single and never in tetrads or larger units. Grains are isopolar in almost all instances. In some cases, *e.g. Hecatostemon* (Figs. 171–172), sculpturing elements consistently on one side of the endoaperture produced anisopolar grains, but it was not possible to distinguish the proximal from the distal end.

Shape of the grains is prolate in most genera, but spheroidal grains are also found. Oblate grains are uncommon in the family.

Wall structure and sculpture pattern were occasionally difficult to determine. In optical cross section, most flacourtiaceous grains appeared to have an outer sculptured portion of the exine about equal in thickness to the non-sculptured exine. This observation is not further repeated and, in terms of phylogenetic studies, is not very meaningful. The thickness of the foot layer and other chemically defined layers are not visible with the light microscope. The terms ektexine and endexine are used when referring to wall layers, since they have been demonstrated to be preferable to other terms (Faegri & Iversen, 1966). Wall thickness usually varies little between the polar and equatorial regions. The total exine thickness in the equatorial region is given in the descriptions.

The patterns of sculpture occasionally caused problems of terminology. Sculpture has been described as "external geometrical features without reference to their internal construction" (Reitsma, 1970*a*: 46), but in the case of reticulate grains it is difficult to separate the two. Most flacourtiaceous grains have a perforated tectum or reticulate pattern in gradual transitions up to per-reticulate. The smallest muri and lumina are near the limits of resolution at 1000 ×. When these patterns were smaller than 1μ, L-O patterns were often helpful in determining the structure. The terms simpli- or duplibaculate are used to describe muri supported by single or double rows of baculae (Columellae), when either condition is visible.

Apertures in the Flacourtiaceae are always meridionally and zonally arranged, the edges being more or less level with the exine. The apertures are almost always compound, consisting of a wide or narrow colpus (ectoaperture) which is lens shaped with pointed ends converging on the polar areas. A distinct aperture-free polar area is always present at both ends. Edges of the colpi are distinct and straight unless noted as being ragged or obscure. An inner aperture (endoaperture, Van Campo, 1958) is usually present and found in the endexine (Figs. 171–172). The equatorially placed endoaperture is usually equatorially elongate beyond the edges of the colpus, often with truncate or indeterminate ends. Distinctness of these apertures is noted in the descriptions and is highly variable. This kind of aperture has been called a "colpus transversales" (Faegri & Iversen, 1964), if it has a length-breadth ratio of greater than 2 (Reitsma, 1970*b*). Endo-



FIGURES 1–15. Pollen of Flacourtiaceae, tribes Berberidopsideae and Oncobeae, × 1000. —1–12. Berberidopsideae.—1–2. *Berberidopsis corallina* (*Philippi s. n.*).—1. Equatorial view of colpus.—2. Polar view, optical cross section and polar surface.—3–4. *Erythrospermum acuminatissimum* (*Smith 1254*).—3. Equatorial view of colpus.—4. Polar view, optical cross section and finely reticulate polar surface.—5–6. *Ahernia glandulosa* (*Loher 5568*).—5. Equatorial view of colpus.—6. Polar view, optical cross section and finely reticulate polar surface. —7–8. *Dasylepis leretii* (*DeGiorgi 1738*).—7. Equatorial view of colpus and pore.—8. Polar

apertures with less than this ratio have been called porae or ora. It has been stated that "a porus is supposed to be nothing more than a short colpus" (Reitsma, 1970*b*: 284), but it has not been demonstrated that the elongate endoaperture described here is homologous with all other types of pores occupying the centers of colpi. Therefore, I will retain the more purely descriptive term "endoaperture" which at least accurately reflects placement in the endexine layer.

Thickenings in the endexine layer bordering the apertures, the costae, occur in most species observed. Costae may outline only the ectoaperture, the endoaperture, both, or may be restricted to the four corners of the intersection of the two apertures. The colpi "membranes" are usually free of sculpturing elements.

A number of genera have colpi with endoapertures being either obscure or absent. Grains are called colporoidate, if the equatorial area of the colpus has lighter optical density or shows a constriction.

The distribution of grain sizes is mostly limited to Erdtman's (1952) categories of small (10–25μ) and medium-sized (25–50μ).

Observations

BERBERIDOPSIDEAE

Berberidopsis Hook. f. Figs. 1–2.

Pollen grains spheroidal to prolate spheroidal. Structure obscure but probably tectate, no baculae seen. Psilate. Exine thickness 1.5μ. Tricolpate, colpi delimitation distinct, not costate. Average size: P = 25–30μ; E = 30–33μ.

Specimen examined: *B. corallina* J. D. Hook.—Chile, *Philippi s. n.* (US).

Erythrospermum Lam. Figs. 3–4.

Pollen grains prolate-spheroidal. Structure obscure but probably tectate. Finely verrucate. Exine thickness 1.5μ. Tricolpate-tricolporoidate. Colpi may be constricted at equator. Faintly costate. Average size: P = 19μ; E = 18μ.

Specimen examined: *E. acuminatissimum* (A. Gray) A. C. Sm.—Fiji, *Smith 1254* (US).

Ahernia Merrill Figs. 5–6.

Pollen grains spheroidal to prolate-spheroidal, semitectate, reticulate, lumen less than 1μ. Exine thickness 1.5μ. Tricolporoidate. Colpi constricted at the equator. Faintly costate. Average size: P = 18–20μ; E = 18μ.

Specimen examined: *A. glandulosa* Merr.—Philippines, *Loher 5568* (US).

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view, optical cross section and finely reticulate polar surface.—9–10. *Scottellia klaineana* (*Klaine 3438*).—9. Equatorial view of pore.—10. Polar view, optical cross section and finely reticulate polar surface.—11–12. *S. coriacea* (*Kennedy 1674*).—11. Equatorial view of pore.—12. Polar view, optical cross section and finely reticulate polar surface.—13–15. Oncobeae. 13–14. *Carpotroche platyptera* (*Kuylen 69x*).—13. Equatorial view of colpus.—14. Polar view, optical cross section and coarsely reticulate surface.—15. *C.* sp. (*Froes 21101*). Equatorial view, internal surface of pore.

Dasylepis Oliv. Figs. 7–8.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen 0.3–0.5μ. Exine thickness 1.5–2μ. Tricolporate, endoapertures rectangular, equatorially elongate. Colpi costate. Average size: P = 25μ; E = 23–25μ.

Specimens examined: *D. lereti* DeWild.—West Africa, *De Giorgi 1738* (US). *D. integra* Warb.—West Africa, *Holst 1220* (US).

Scottellia Oliv. Figs. 9–12.

Pollen grains spheroidal, semitectate, reticulate. Baculae not visible, lumen less than 1μ. Exine thickness 1.5μ. Tricolporate, endoapertures rectangular, costate, equatorially elongate. Average size: P = 18–20μ; E = 18–20μ.

Specimens examined: S. *coriacea* A. Chev.—Nigeria, *Kennedy 1674* (US). S. *klaineana* Poire—Gabon, *Klaine 3438* (US).

ONCOBEAE

Carpotroche Endl. Figs. 13–15.

Pollen grains spheroidal, semitectate, finely reticulate to duplibaculate and per-reticulate, lumen 0.1–4μ. Exine thickness 1.5–4μ. Tricolpor(-oid-)ate, endoapertures may be costate but faintly delimited. Average size: P = 37–40μ; E = 37–40μ.

Specimens examined: *C. platyptera* Pittier—Honduras, *Kuylen 69x* (US). *C.* sp.—Brazil, *Fróes 21101* (US).

Mayna Aubl. Figs. 16–19.

Pollen grains spheroidal, semitectate, reticulate or per-reticulate, simpli- or duplibaculate. Lumen 1–4.5μ. Exine thickness 1.5–2.5μ. Tricolpor(-oid-)ate. Colpi costate near endoapertures, delimitation of endoapertures diffuse. Average size: P = 33–50μ; E = 33–46μ.

Specimens examined: *M. echinata* Spruce—Peru, *Klug 3808* (US). *M. longifolia* P. &. E. var *heliocarpa* R. E. Schult.—Brazil, *Schultes 6593* (US). *M. odorata* Aubl.—Brazil, *Ducke 15156* (US).

Oncoba Forsk. Figs. 20–21.

Pollen grains prolate-spheroidal, semitectate, reticulate to per-reticulate, simplibaculate. Lumen 0.5–1.5μ. Exine thickness 1–2μ. Tricolporoidate, costate, endoaperture delimitation diffuse. Average size: P = 20–30μ; E = 20–30μ.

→

FIGURES 16–29. Pollen of Flacourtiaceae, tribe Oncobeae, × 1000.—16–17. *Mayna longifolia* (*Schultes 6593*).—16. Equatorial view showing colpus and pore.—17. Polar view, optical cross section and coarsely reticulate, duplibacculate polar surface.—18–19. *M. odorata* (*Ducke 15156*).—18. Equatorial view of pore.—19. Polar view, optical cross section and reticulate polar surface.—20–21. *Oncoba spinosa* (*Jack 6549*).—20. Equatorial view of colpus.—21. Polar view, optical cross section and reticulate polar surface.—22–23. *Caloncoba echinata* (*Jack 4744*).—22. Equatorial view of colpus divided by an equatorial bridge.—23. Polar view, optical cross section and reticulate polar surface.—24–25. *Lindackeria dentata* (*Lebrun 6780*).—24. Equatorial view of colpus.—25. Polar view, optical cross section and finely reticulate polar surface.—26–27. *Poggea kameruunensis* (*Zenker 239*).—26. Equatorial view, internal surface at pore.—27. Polar view, optical cross section and reticulate polar surface.—28–29. *Buchnerodendron speciosum* (*Robyns 1336*).—28. Equatorial view.—29. Polar view, optical cross section and polar surface.

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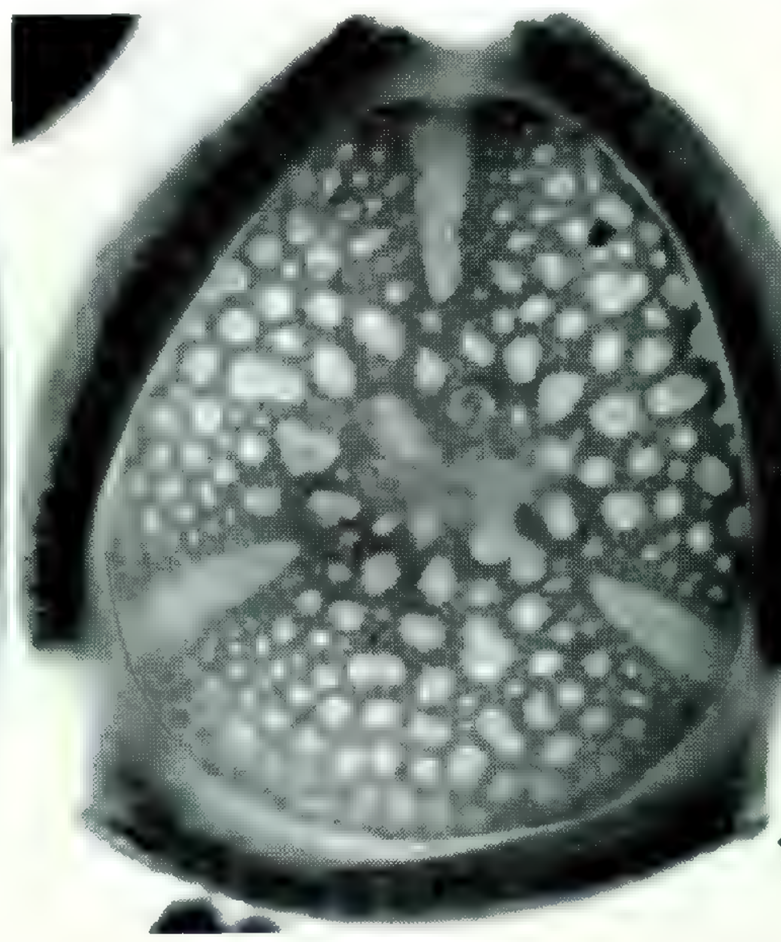

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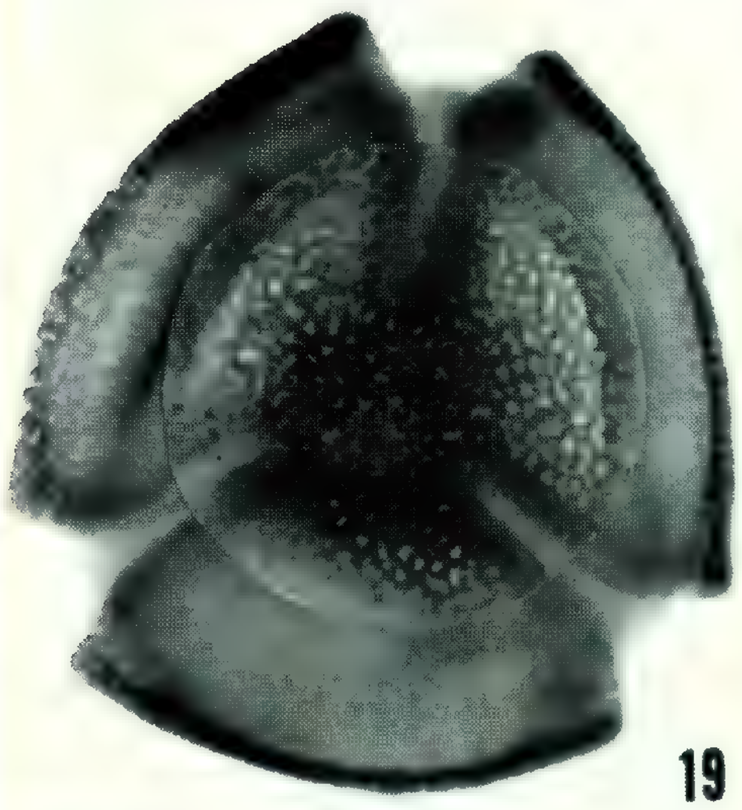

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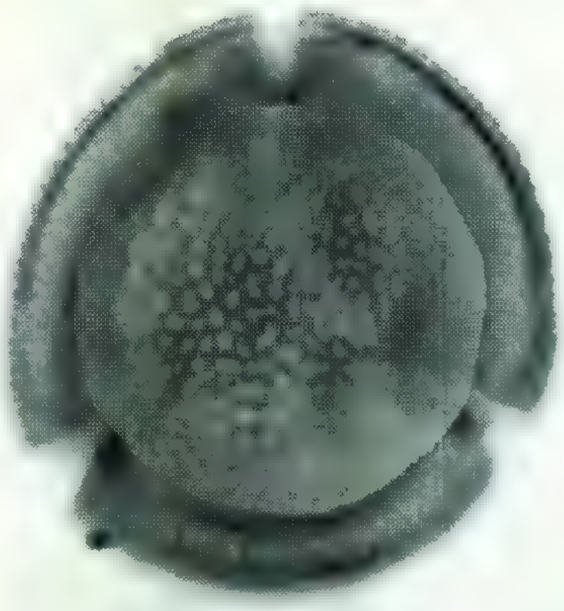

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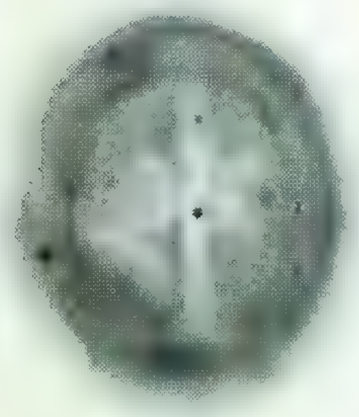

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Specimens examined: *O. laurina* (Presl) Warb.—Panama, *Allen 3665* (US). *O. spinosa* Forsk.—Cuba, *Jack 6549* (US).

Caloncoba Gilg Figs. 22–23.

Pollen grains prolate-spheroidal, tectate, reticulate to finely reticulate, simplibaculate, lumen 0.1–0.5μ. Exine thickness 1–2μ. Tricolporoidate, colpi divided transversely by a bridge in the ektexine. Average size: P = 20–38μ; E = 23–35μ.

Specimens examined: *C. brevipes* Gilg—Ghana, *Fairchild 1223* (US). *C. echinata* (Oliv.) Gilg—Cuba, *Jack 4744* (US). *C. glauca* (Oliv.) Gilg—Congo, *Robyns 1194* (US).

Lindackeria Presl Figs. 24–25.

Pollen grains prolate-spheroidal to prolate, semitectate or tectate, reticulate to finely reticulate, lumen 0.2–1μ. Exine thickness 1.5–2μ. Tricolporoidate, costate in some specimens, delimitation of endoapertures may be diffuse. Average size: P = 18–30μ; E = 18–30μ.

Specimens examined: *L. dentata* (Oliv.) Gilg—Central Africa, *Troupin 6362* (US). Congo, *Lebrun 6780* (US). *L. paludosa* (Benth.) Gilg—Venezuela, *Holt & Blake 693* (US). *L. Poggei* (Gürke) Gilg—Congo, *Gossweiler 8664* (US).

Poggea Gürke Figs. 26–27.

Pollen grains prolate-spheroidal. Structure tectate, reticulate, simplibaculate. Lumen 0.7–1μ. Exine thickness 1.5μ. Tricolporate, occasionally tetracolporate, endoaperture equatorially elongate with transverse costae. Endoaperture delimitation diffuse at ends. Average size: P = 28–30μ; E = 25–28μ.

Specimen examined: *P. kameruunensis* Gilg—Cameroons, *Zenker 239* (US).

Buchnerodendron Gürke Figs. 28–29.

Pollen grains spheroidal, tectate, finely reticulate, lumen 0.2–0.5μ. Exine thickness 1μ. Tricolpate, tricolporoidate. Apertures diffuse and difficult to orient. Average size: P = 18–20μ; E = 18–20μ.

Specimen examined: *B. speciosum* Gürke—Congo, *Robyns 1336* (US).

SCOLOPIEAE

Scolopia Schreb. Figs. 30–34.

Pollen grains prolate spheroidal to prolate, tectate, reticulate, lumen 0.3–1μ. Exine thickness 1–2μ. Tricolporoidate, colpi costate, endoapertures diffuse at edges. Average size: P = 23–25μ; E = 18–23μ.

Specimens examined: *S. brownii* F. v. M.—Australia, *Leonhardt s. n.* (US). *S. cochinchinensis* (Lour.) Clos—Viet Nam, *Clemans 3833* (US). *S. eckloni* Szysz.—South Africa, *Wood s. n.* (US). *S. luzonensis* Warb.—Philippines, *Elmer 5625* (US). *S. oldhamii* Hance—Formosa, *Wilson 10781* (US).

BANAREAE

Banara Aubl. Figs. 35–37.

Pollen grains prolate-spheroidal, tectate, reticulate. Lumen 0.5–1μ. Exine thickness 1μ. tricolpor(-oid-)ate, costate, endoapertures diffuse, equatorially

elongate. Average size: P = 15–28μ; E = 13–23μ.—This description does not apply to *B. costaricensis* Figs. 44–45.

Specimens examined: *B. guiinensis* Aubl.—Venezuela, *Pittier 11606* (US). *B. mollis* Tul.—Peru, *Klug 3301* (US). *B. costaricensis* (Standl.) Sleumer.—Costa Rica, *Holm & Iltis 787* (US).

Pineda Ruiz & Pav. Figs. 40–41.

Pollen grains prolate-spheroidal, tectate, simplibaculate, reticulate; lumen 0.5μ. Exine thickness 2μ. Tricolporoidate, colpi costate; equatorial bridge in the ektexine may replace diffuse endoaperture. Average size: P = 23–25μ; E = 18–20μ.

Specimen examined: *P. incana* R. & P.—Peru, *Vargas 7596* (US).

Trimeria Harv. Figs. 42–43.

Pollen grains prolate, tectate, reticulate. Lumen 1–1.5μ. Exine thickness 1.3–2μ. Tricolporate to tricolporoidate, costate, endoapertures equatorially elongate or replaced by an equatorial bridge in the ektexine. Average size: P = 18–20μ; E = 13–15μ.

Specimen examined: *T. alnifolia* Planch.—Praetoria, *Ratray 313* (US).

Pleuranthodendron L. O. Wms. Figs. 38–39.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.5–1μ. Exine thickness 1μ. Tricolpor(-oid-)ate, costate, endoapertures diffuse. Average size: P = 15–18μ; E = 13–15μ.

Specimen examined: *P. mexicana* (A. Gray) L. O. Wms.—Mexico, *Mexia 9284* (US).

HOMALIEAE

Dissomeria Benth. Figs. 46–47.

Pollen grains prolate, tectate, reticulate, lumen 0.3μ. Exine thickness 2μ. Apertures tricolporate, costate, endoapertures equatorially elongate. Average size: P = 25–30μ; E = 20–25μ.

Specimen examined: *D. crenata* Benth.—Ghana, *Vique 1550* (US).

Calantica Jaub. *ex.* Tul. Figs. 48–49.

Pollen grains prolate, tectate, finely reticulate, lumen 0.7–1μ. Exine thickness 2μ. Tricolporate, costate, endoapertures equatorially elongate, edges diffuse. Average size: P = 28–30μ; E = 20–23μ.

Specimen examined: *C. ceratifolia* Endl.—Madagascar, *Hildebrandt 3817* (US).

Homalium Jacq. Figs. 52–59.

Pollen grains prolate, tectate, finely reticulate to obscure, lumen 0.3–1μ. Exine thickness 1.5–2μ. Tricolporate, costate, endoapertures equatorially elongate with constricted, or branched, indeterminate ends. Occasional ektexine elements on the colpi membrane above or below endoapertures. Average size: P = 15–35μ; E = 13–25μ.

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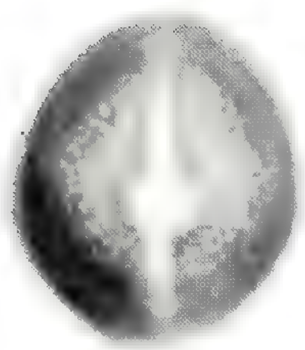
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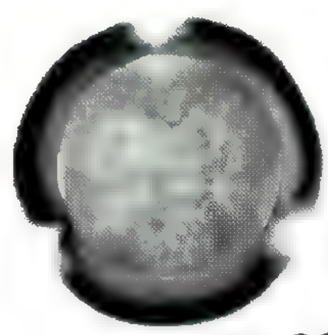
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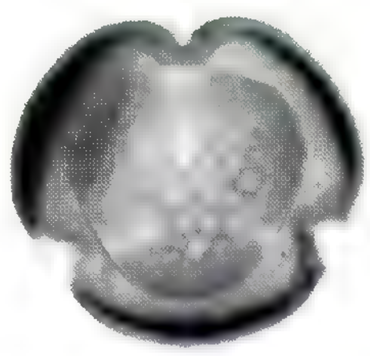
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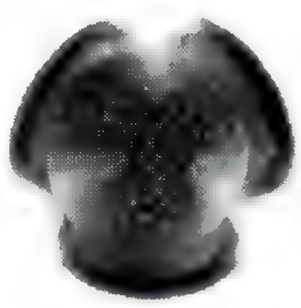
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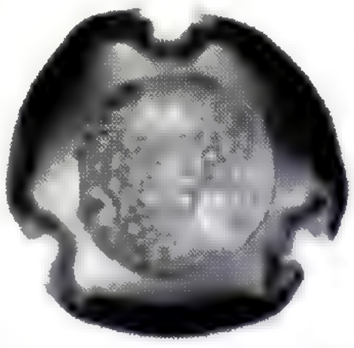
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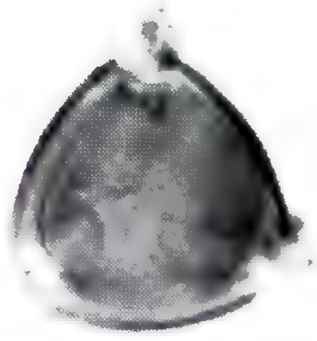
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Specimens examined: *H. bracteatum* Benth.—Philippines, *Darling 18691* (US). *H. cochinchinensis* (Lour.) Druce—Hong Kong, *Taam 2015* (US). *H. deplanchei* Warb.—New Caledonia, *McKee 7963* (US). *H. guianense* (Aubl.) Warb.—British Guiana, *Smith 2664* (US). *H. hainanense* Gagnep.—China, *Lei 399* (US). *H. hosei* Merr.—Borneo, *Ramos 1174* (US). *H. humblotii* H. Bn.—Madagascar, *Humblot 582* (US). *H. involucratum* (DC.) H. Bn.—Madagascar, *Hildebrandt 3310* (US). *H. nepaulense* (DC.) Benth.—Nepal, *Nicolson 2504* (US). *H. racemosum* Jacq.—Panama, *Pittier 2693* (US). *H. stenophyllum* Merr. & Chun—China, *Chun & Tso 43732* (US). *H. stipulaceum* Welw.—Congo, *Gossweiler 8525* (US). *H. tomentosum* (Vent.) Benth.—Burma, *Mikee 5969* (US).

Gerrardina Oliv. Figs. 50–51.

Pollen grains spheroidal, subangulaperturate, tectate, finely reticulate, lumen 0.5–1.2μ. Exine thickness 1μ. Tricolpor-(oid-)ate, costate, endoapertures diffuse, equatorially elongate. Average size: P = 13–15μ; E = 13–15μ.

Specimens examined: *G. eylesiana* Milne-Redh.—Nyasaland, *Brass 16641* (US).

PANGIEAE

Hydnocarpus Gaertn. Figs. 62–63.

Pollen grains spheroidal, semitectate, per-reticulate, simplibaculate, lumen 2–6μ. Exine thickness 4.5μ. Tricolporate, costae not visible, endoapertures probably equatorially elongate but obscured by heavy reticulum. Average size: P = 33–43μ; E = 33–35μ.

Specimens examined: *H. calophylla* (Ridl.) Sleum.—Borneo, *Jacobs 5181* (US). *H. ilicifolia* King—Viet Nam, *Petelot s. n.* (US). *H. wightiana* Blume—Brazil, *Krug 4315* (US).

Pangium Reinw. Figs. 67–68.

Pollen grains oblate-spheroidal. Exine with perforated tectum with uniformly closely spaced baculae visible. No measurable lumen. Exine thickness 1.5–2μ. Tricolporate, endoapertures equatorially elongate with margins having baculate proliferations. Colpi obscure. Average size: P = 33–38μ; E = 40–45μ.

Specimen examined: *P. edule* Reinw.—New Guinea, *Brass 27673* (US).

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FIGURES 30–51. Pollen of Flacourtiaceae, tribes Scolopieae, Banareae, and Homalieae, × 1000.—30–34. Scolopieae.—30–31. *Scolopia cochinchinensis* (*Clemens 3833*).—30. Equatorial view of colpus.—31. Polar view, optical cross section and reticulate polar surface.—32. S. *brownii* (*Leonhardt s. n.*), equatorial view of colpus.—33–34. S. *luzonensis* (*Elmer 5625*).—33. Equatorial view.—34. Polar view, optical cross section and polar surface.—35–45. Banareae.—35–36. *Banara guiinensis* (*Pittier 11606*).—35. Equatorial view of colpus and pore.—36. Polar view, optical cross section and finely reticulate polar surface.—37. *B. mollis* (*Klug 3301*), equatorial view of colpus.—38–39. *Pleuranthodendron mexicana* (*Mexia 9284*).—38. Equatorial view of colpus.—39. Polar view, optical cross section and finely reticulate polar surface.—40–41. *Pineda incana* (*Vargas 7596*).—40. Equatorial view of colpus.—41. Polar view, optical cross section and reticulate polar surface.—42–43. *Trimeria alnifolia* (*Ratray 313*).—42. Equatorial view showing colpus.—43. Polar view, optical cross section and finely reticulate polar surface.—44–45. *Banara costaricensis* (*Holm & Iltis 787*).—44. Equatorial view of colpus and pore.—45. Polar view, optical cross section and polar surface.—46–51. Homalieae.—46–47. *Dissomeria crenata* (*Vique 1550*).—46. Equatorial view of colpus and costae.—47. Polar view, optical cross section and finely reticulate polar surface.—48–49. *Calantica ceratifolia* (*Hildebrandt 3817*).—48. Equatorial view of colpus.—49. Polar view, optical cross section and finely reticulate polar surface.—50–51. *Gerradina eylesiana* (*Brass 16641*).—50. Equatorial view with colpus.—51. Polar view, optical cross section and polar surface.

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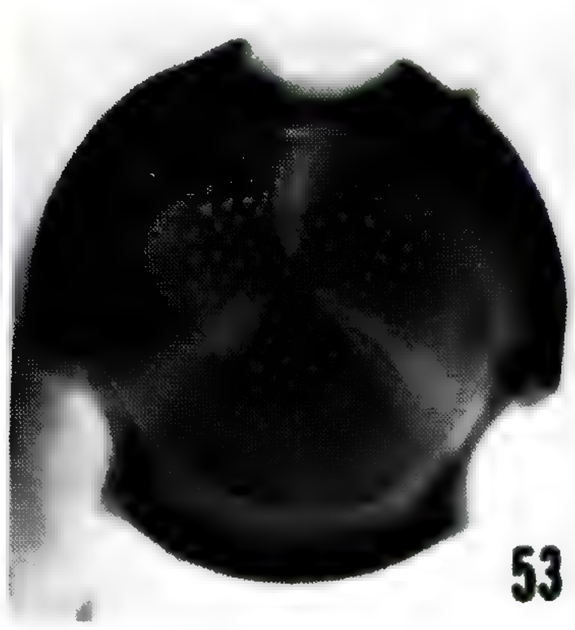
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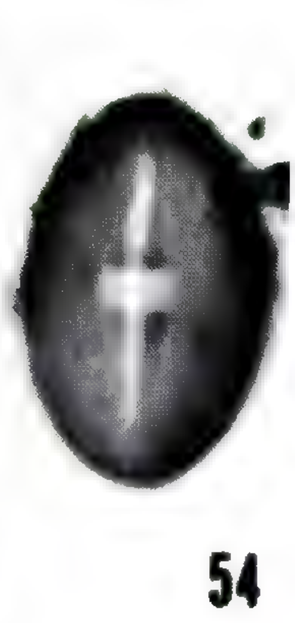
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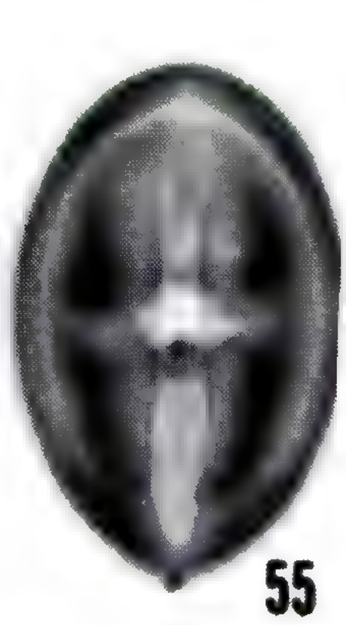
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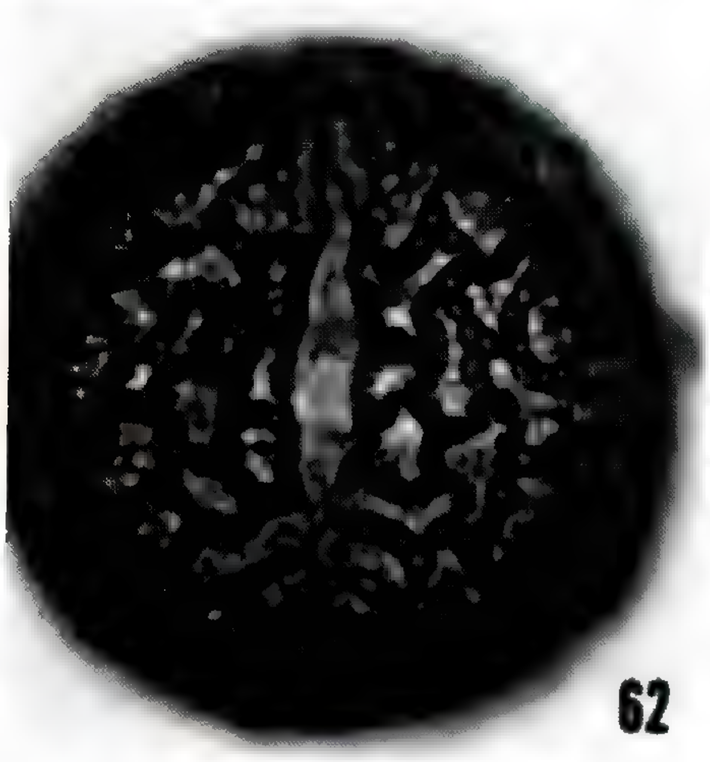
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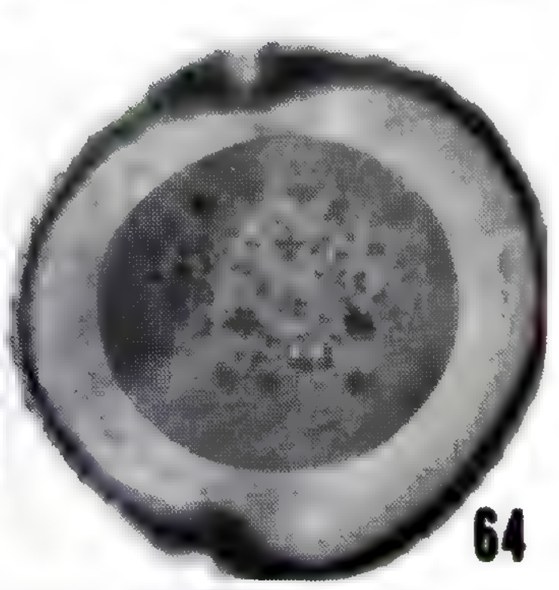
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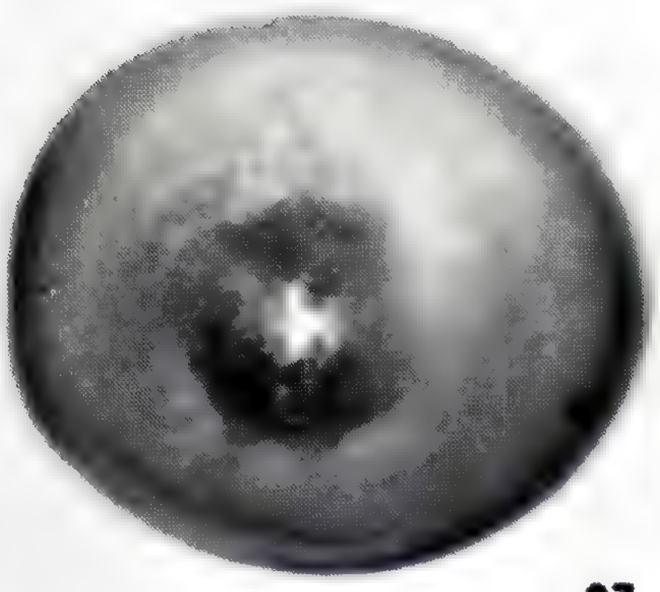
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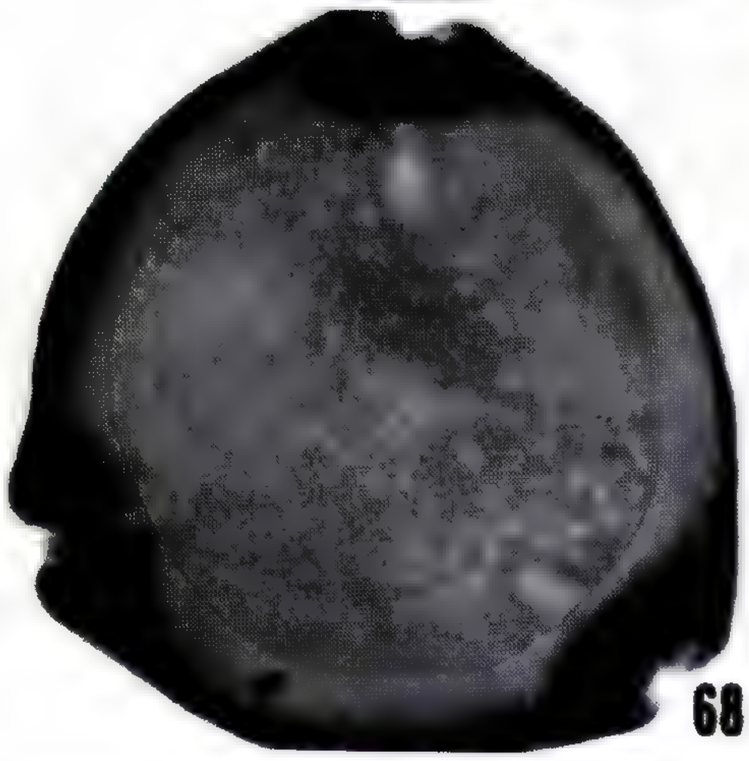
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FIGURES 52–68.—Pollen of Flacourtiaceae, tribes Homalieae and Pangieae, × 1000.—52–59. Homalieae.—52–53. *Homalium racemosum* (*Pittier 2693*).—52. Equatorial view with colpus and pore.—53. Polar view, optical cross section and reticulate polar surface.—54. *H. humblotii* (*Humblot 582*), equatorial view with colpus and pore.—55–56. *H. bracteatum* (*Darling 18691*).—55. Equatoral view with colpus and pore.—56. Polar view, optical cross section and finely reticulate polar surface.—57–58. *H. guianense* (*Smith 2664*).—57. Equatorial view with colpus and pore.—58. Polar view, optical cross section and finely reticulate polar surface.—59. *H. hainanensis* (*Lei 399*), equatorial view.—60–68. Pangieae.—60–61. *Trichadenia philippinensis* (*Ahern 2982*).—60. Equatorial view with colpus.—61. Polar view,

Trichadenia Thw. Figs. 60–61.

Pollen oblate-spheroidal, intectate, baculate and verrucate in a mixed, random pattern. Bacules to 3μ high, verrucae to 4μ wide and high. Exine thickness 5–6μ. Tricolporate, costate, endoapertures distinct and variable. Colpi diffuse. Average size: P = 33–38μ; E = 40–45μ.

Specimen examined: *T. philippensis* Merr.—Philippines, *Ahern 2982* (US).

Ryparosa Bl. Figs. 64–66.

Pollen grains prolate-spheroidal, tectate, finely reticulate, lumen 0.2–0.5μ. Exine thickness 1.5–2μ. Tri (bi-)colpate or tricolporate, endoapertures distinct, the margins with small processes extending over the opening. Colpi diffuse. Average size: P = 20–27μ; E = 18–23μ.

Specimens examined: *R. acuminata* Merr.—Borneo, *Ramos 1367* (US). *R. hirsuta* J. J. Sm.—Borneo, *Agama 662* (US). *R. wrayi* King—Sumatra, *Bartlett 8410* (US).

Kiggelaria L. Figs. 69–71.

Pollen grains prolate to prolate-spheroidal, tectate with a finely granular pattern. Exine thickness 2–2.5μ. Tricolpor(-oid-)ate, endoapertures constricted or equatorially elongate. Costae prominent. Average size: P = 30–45μ; E = 33 = 45μ.

Specimens examined: *K. africana* L.—Transvaal, *Schlieben 7341* (US). *K. integrifolia* Jacq.—South Africa, *Ecklon & Zeyler s. n.* (US).

FLACOURTIEAE

Bennettiodendron Merrill Figs. 72–73.

Pollen grains subprolate, semitectate, reticulate, lumen 0.5–1.5μ. Exine thickness 1.5μ. Tricolpor(-oid-)ate, weakly costate, endoapertures equatorially elongate with diffuse ends. Ends of colpi occasionally connect over poles. Average size: P = 18–20μ; E = 18–20μ.

Specimen examined: *B. leprosipes* (Clos) Merr.—Sumatra, *Toroes 3329* (US).

Flacourtia L'Herit. Figs. 74–76.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.8–1.5μ. Exine thickness 1–1.5μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Average size: P = 15–25μ; E = 13–20μ.

Specimens examined: *F. euphlebia* Merr.—Philippines, *Burnea 28968* (US). *F. indica* (Burm. f.) Merr.—Cuba, *Jack 4961* (US). *F. mollis* Hook & Grev.—Burma, *Rock 2158* (US). *F. ramontchii* L'Herit.—India, *Loelz 4234* (US). Tanganjika, *Schlieben 5465* (US). *F. rukam* Zoll.—Sumatra, *Bartlett 8714* (US). *F. sepiaria* Roxb.—Philippines, *Ramos 3317* (US). *F. subintegra* A. C. Sm.—Fiji, *Smith 6793* (US).

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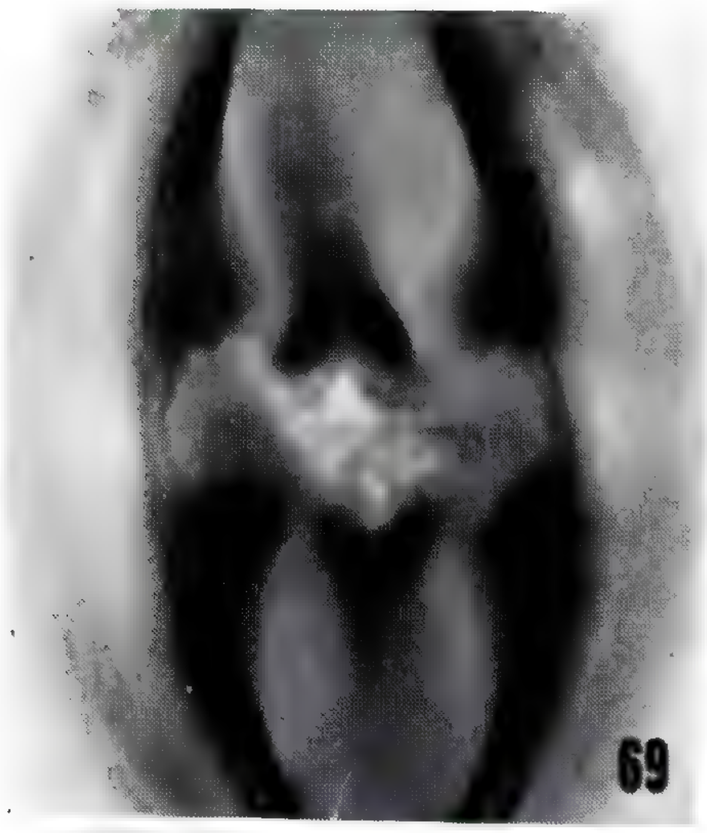
optical cross section and verrucate polar surface.—62–63. *Hydnocarpus calophylla* (*Jacobs 5181*).—62. Equatorial view with colpus and pore.—63. Polar view, optical cross section and coarsely reticulate, simplibacculate polar surface.—64–66. *Ryparosa wrayi* (*Bartlett 8410*). —64. Polar view, optical cross section, bicolpate, and polar surface.—65. Equatorial view with pore.—66. Equatorial view with pore.—67–68. *Pangium edule* (*Brass 27673A*).—67. Equatorial view with pore.—68. Polar view, optical cross section and polar surface.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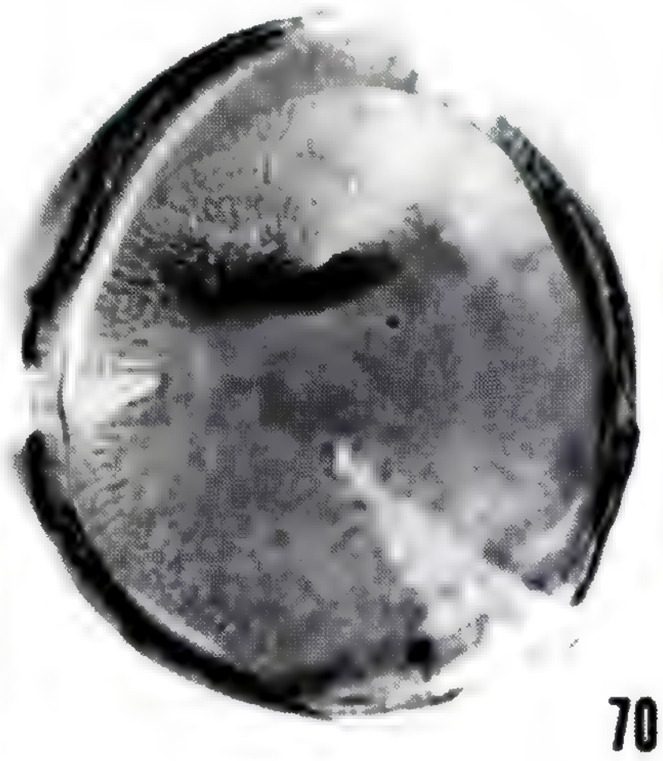
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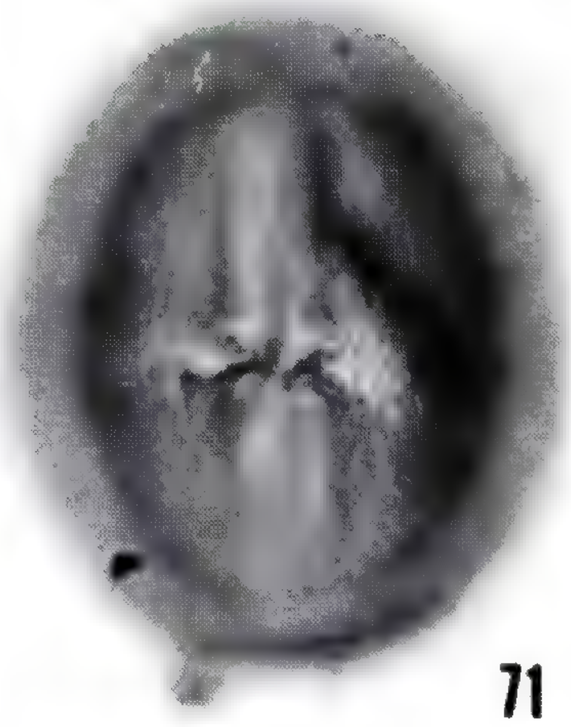
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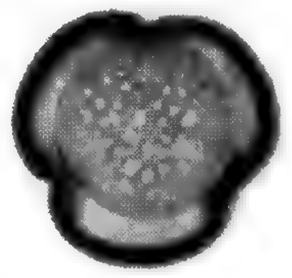
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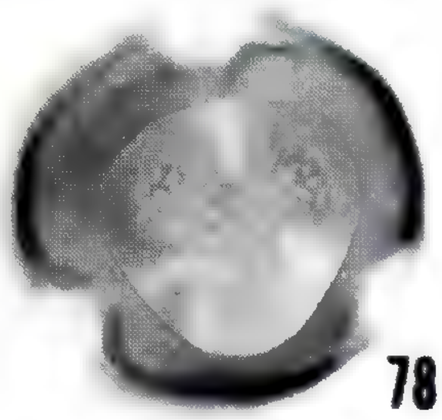
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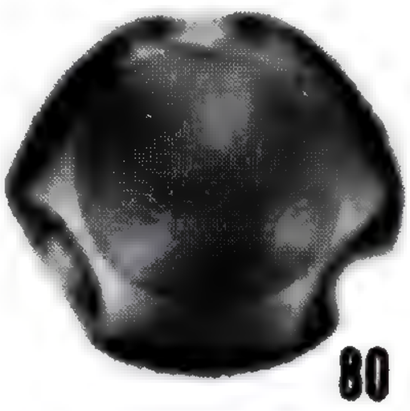
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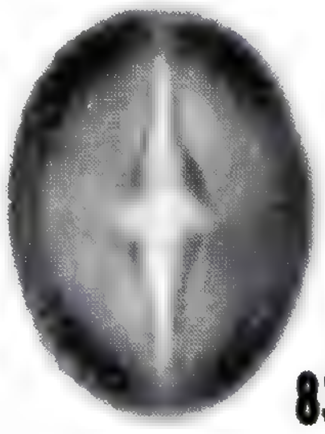
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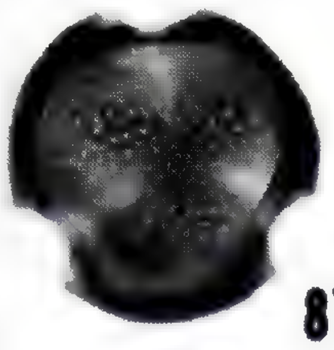
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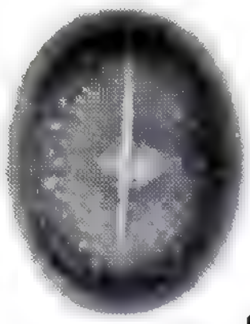
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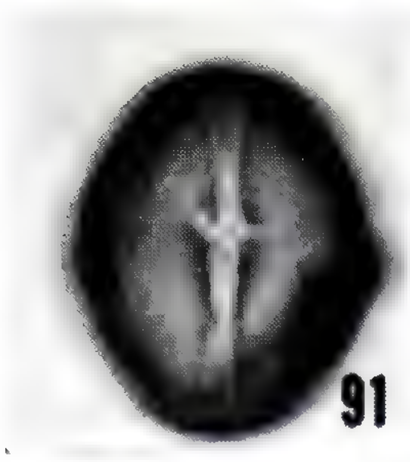
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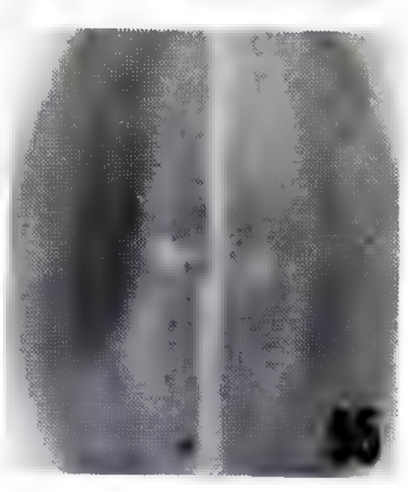
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Dovyalis E. Mey. *ex* Arn. Figs. 77–78.

Pollen grains spheroidal, tectate, reticulate, lumen 0.8–2.0μ. Exine thickness 1.2μ. Tricolporate, weakly costate, endoapertures equatorially elongate. Average size: P = 25–28μ; E = 23–25μ.

Specimen examined: *D. abyssinica* (A. Rich.) Warb.—Kenya, *Geesteranus 5361* (US).

Aphloia Benn. Figs. 79–80.

Pollen grains spheroidal, interhexagonal to spherical in polar view, intectate, striate, lumen 0.8μ. Exine thickness 1.5–2μ. Tricolporate with large elliptical, equatorially elongate endoapertures. Colpi diffuse, weakly costate. Average size: P = 20–25μ; E = 20–25μ.

Specimen examined: *A. thaeaformis* subsp. *madagascariensis* var. *minima* (Bak.) H. Perr.—Madagascar, *Humbert 6175* (US).

Azara Ruiz & Pav. Figs. 81–82.

Pollen grains prolate, tectate, reticulate, lumen 0.8–1.5μ. Exine thickness 1.5–2μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate with diffuse ends. Scattered costal thickenings in the vicinity of the endoapertures in some specimens. Average size: P = 18–25μ; E = 15–20μ.

Specimens examined: *A. bergii* Phil.—Chile, *Claude-Joseph 1445* (US). *A. integrifolia* Ruiz & Pav.—Chile, *Werdermann 1386* (US). *A. lanceolata* Hook. f.—Chile, *Claude-Joseph 2411* (US). *A. serrata* Ruiz & Pav.—Chile, *Rose 19366* (US).

Xylosma Forst f. Figs. 83–88.

Pollen grains prolate to prolate-spheroidal, tectate, reticulate, lumen 0.5–1.5μ. Exine thickness 1–2μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially

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FIGURES 69–95. Pollen of Flacourtiaceae, tribes Pangieae and Flacourtieae, × 1000.—69–71. Pangieae.—69–70. *Kiggelaria africana* (*Schlieben 7341*).—69. Equatorial view with pore and costae.—70. Polar view, optical cross section and polar surface.—71. *K. integrifolia* (*Ecklon & Zeyler s. n.*), equatorial view.—72–95. Flacourtieae.—72–73. *Bennettiodendron leprosipes* (*Toroes 3329*).—72. Equatorial view with colpus.—73. Polar view, optical cross section and reticulate polar surface.—74. *Flacourtia euphlebia* (*Burnea 28986*), equatorial view with colpus and pore.—75–76. *F. rukam* (*Bartlett 8714*).—75. Equatorial view with colpus.—76. Polar view, optical cross section and reticulate polar surface.—77–78. *Dovyalis abyssinica* (*Geesteranus 5361*).—77. Equatorial view with pore.—78. Polar view, optical cross section with reticulate polar surface.—79–80. *Aphloia theaeformis* (*Humbert 6175*).—79. Equatorial view with pore.—80. Polar view, optical cross section and polar surface.—81–82. *Azara bergii* (*Claude-Joseph 1445*).—81. Equatorial view with colpus.—82. Polar view, optical cross section and finely reticulate polar surface.—83–84. *Xylosma fawcettii* (*Britton 1311*).—83. Equatorial view with colpus.—84. Polar view, optical cross section and polar surface.—85. *X. spiculiferum* (*Schiefer 593*), equatorial view with colpus and pore.—86–87. *X. luzonensis* (*Ramos & Deroy 22579*).—86. Equatorial view with colpus.—87. Polar view, optical cross section and polar surface.—88. *X. hawaiiense* (*Hitchcock 15280*), equatorial view with colpus and costae.—89–90. *Poliothyrsis sinensis* (*Wilson 500*).—89. Equatorial view with colpus and pore.—90. Polar view, optical cross section and polar surface.—91–92. *Carrieria calycina* (*Wilson 1104*).—91. Equatorial view with colpus and pore.—92. Polar view, optical cross section and polar surface.—93–94. *Itoa stapfii* (*Hoogland 5079*).—93. Equatorial view with colpus and pore.—94. Polar view, optical cross section and polar surface.—95. *I. orientalis* (*Henry 10703*), equatorial view with colpus and pore.

elongate, distinct, with diffuse ends. Colpi and endoapertures may be constricted. Sculpturing elements occasionally found on colpi membranes when endoapertures absent. Average size: P = 18–25μ; E = 15–25μ.

Specimens examined: *X. blepharodes* Lundell—Texas, *Barber 14a* (US). *X. ciliatifolium* (Clos) Eichl.—Brazil, *Pickel 3221* (US). *X. fawcettii* Urb.—Jamaica, *Britton 1311* (US). *X. flanganii* Bolus—Pretoria, *Flangan 682* (US). *X. flexuosa* Hemsl.—Guatemala, *Skutch 348* (US). *X. hawaiiense* Seem.—Hawaii, *Hitchcock 15280* (US). *X. longifolium* Clos—China, *Henry 12635* (US). *X. luzonensis* (Presl) Clos—Philippines, *Ramos & Deroy 22579* (US). *X. orbiculata* Forst.—Tonga, *Yunker 16235* (US). *X. racemosum* Miq.—China, *Levine 1816* (US). *X. spiculiferum* (Yul.) Tr. & Pl.—Colombia, *Schiefer* 593 (US). *X. venosum* N. E. Br. —Argentina, *Schwarz 475* (US).

Poliothyrsis Oliv. Figs 89–90.

Pollen grains prolate, tectate, reticulate, lumen 0.5–1μ. Exine thickness 2.5μ. Tricolporate, costate, endoapertures equatorially elongate. Average size: P = 18–20μ; E = 15–18μ.

Specimen examined: *P. sinensis* Oliv.—China, *Wilson 500* (US).

Carrierea Franch. Figs. 91–92.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1.3μ. Tricolpor(-oid-)ate, costate, endoapertures equatorially elongate, irregular. Average size: P = 23–25μ; E = 18–20μ.

Specimen examined: *C. calycina* Franch.—China, *Wilson 1104* (US).

Itoa Hemsl. Figs. 93–95.

Pollen grains prolate-spheroidal, tectate, reticulate, lumen 0.5–1μ. Exine thickness 1–1.5μ. Tricolporate, costate, endoapertures equatorially elongate with diffuse ends. Average size: P = 18–43μ; E = 15–30μ.

Specimens examined: *I. orientalis* Hemsl.—China, *Henry 10703* (US). *I. stapfii* (Koord.) Sleum.—New Guinea, *Hoogland 5079* (US).

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FIGURES 96–115. Pollen of Flacourtiaceae, tribes Flacourtieae and Casearieae, × 1000.—96–97. Flacourtieae. *Idesia polycarpa* (*Forest 17558*).—96. Equatorial view with colpus.—97. Polar view, optical cross section and reticulate polar surface.—98–115. Casearieae.—98–99. *Casearia graveolens* (*Rock 2839*).—98. Equatorial view with colpus.—99. Polar view, optical cross section, and polar surface.—100–101. *C. cambessedessii* (*Haught 2828*).—100. Equatorial view of interior surface, pore and colpus.—101. Polar view, optical cross section and polar surface.—102–103. *C. javitensis* (*Killip & Smith 30153*).—102. Equatorial view, pore and colpus.—103. Polar view, optical cross section and polar surface.—104–105. *C. floribunda* (*Gossweiler 718*).—104. Equatorial view.—105. Polar view, optical cross section and polar surface.—106. *C. tomentosa* (*Stewart 13756*), equatorial view of interior surface, pore and colpus.—107–108. *C. aculeata* (*Rouirosa 568*).—107. Equatorial view of interior surface, pore and colpus.—108. Polar view, optical cross section and polar surface.—109–110. *C. bahamensis* (*Britton, Cowell & Earle 10300*).—109. Equatorial view colpus and pore.—110. Polar view, optical cross section of tetracolporate grain and polar surface.—111–112. *C. fuliginosa* (*Cuming 1240*).—111. Equatorial view.—112. Polar view, optical cross section and polar surface.—113–114. *C. disticha* (*Degener & Ordonez 13588*).—113. Equatorial view, colpus and pore.—114. Polar view, optical cross section and polar surface.—115. *C. aequilateralis* (*Lau* 39), equatorial view with colpus and pore.

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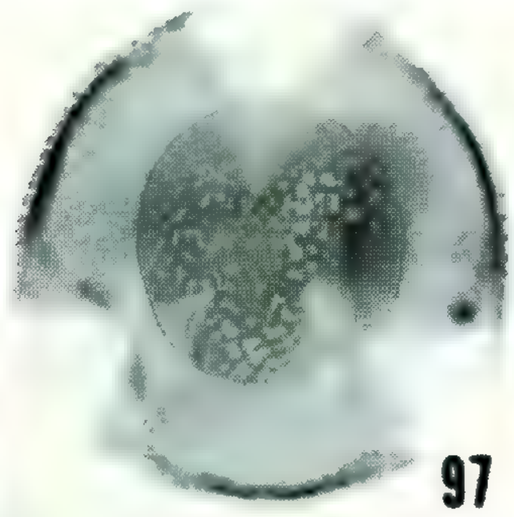
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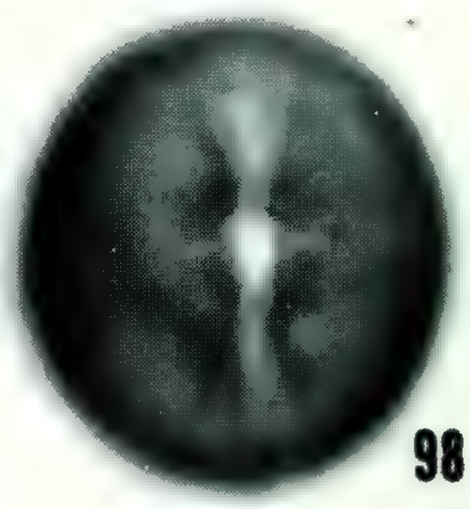
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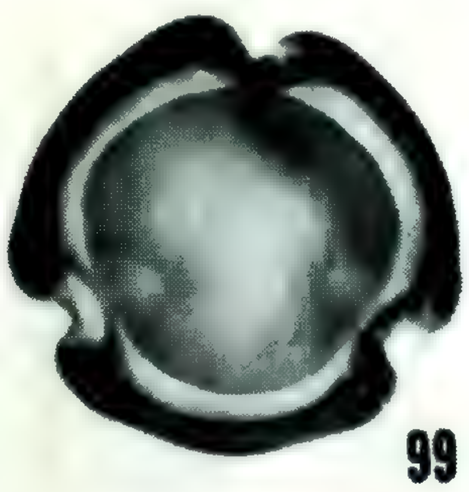
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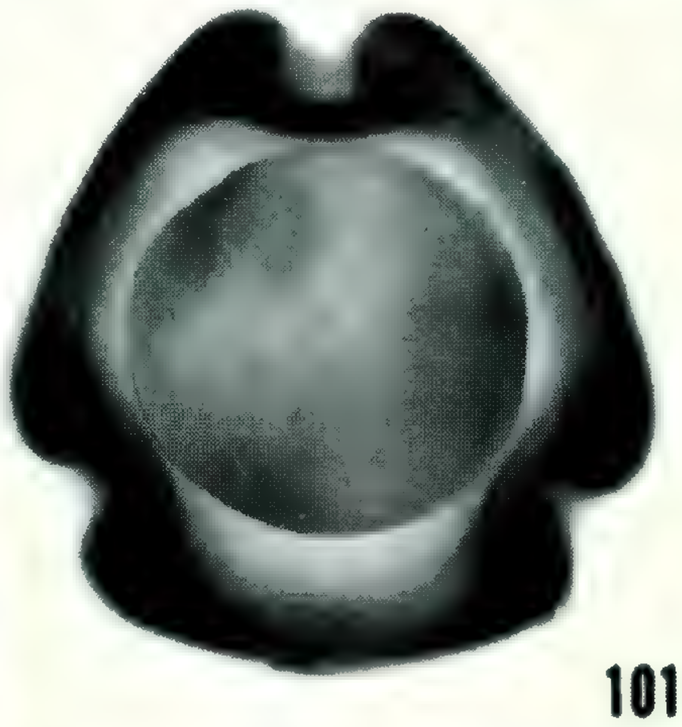
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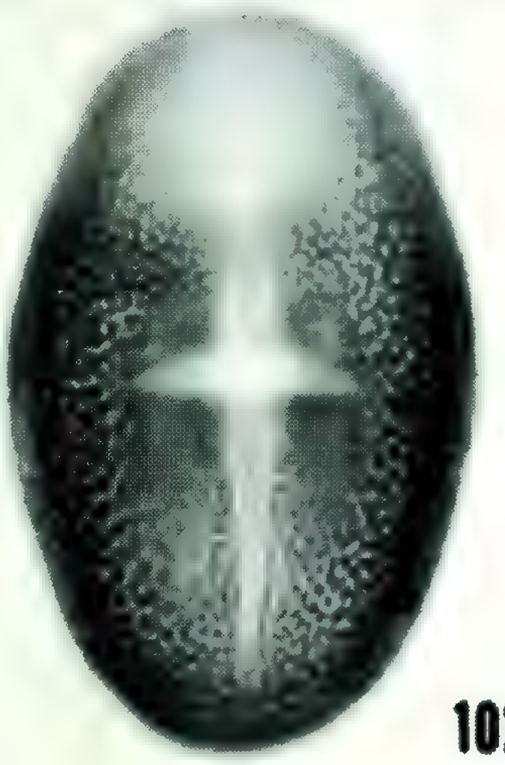
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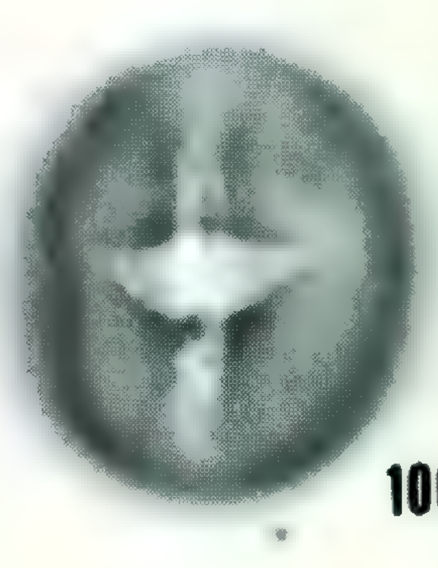
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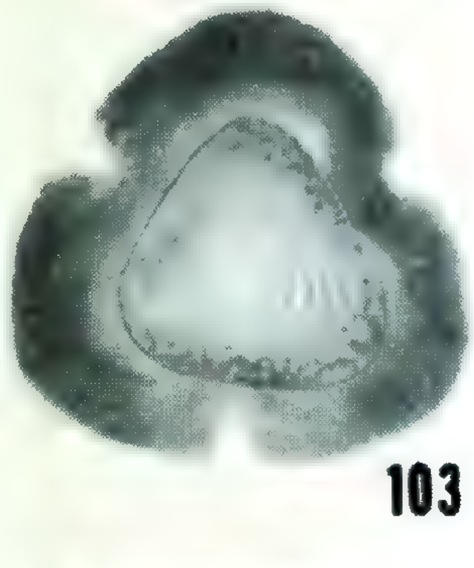
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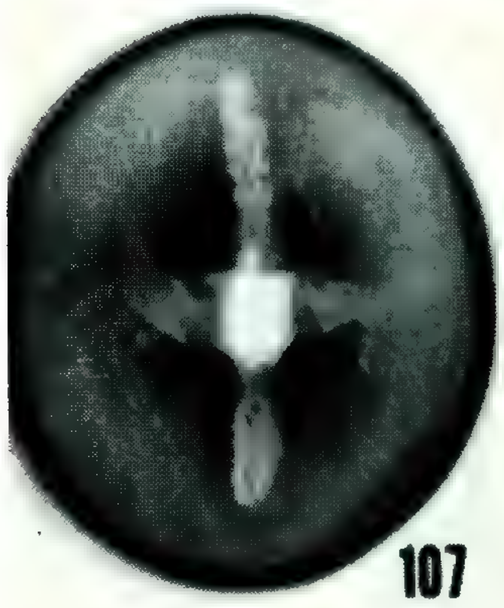
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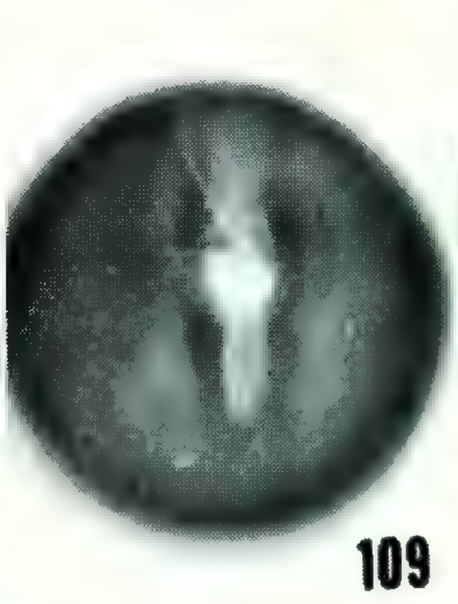
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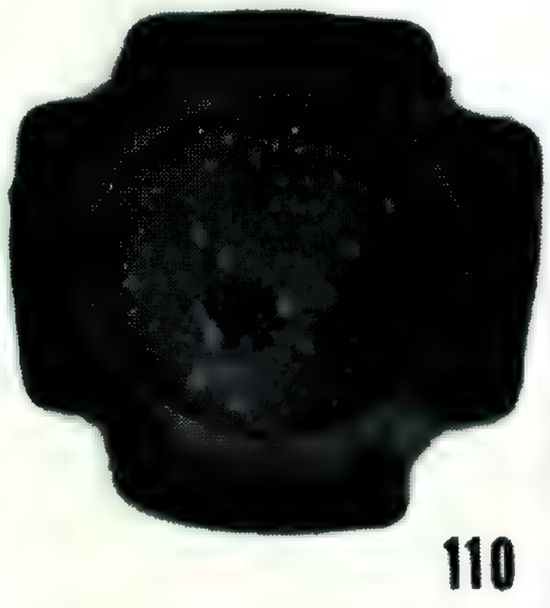
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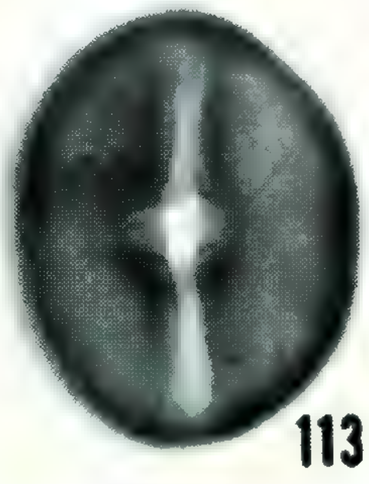
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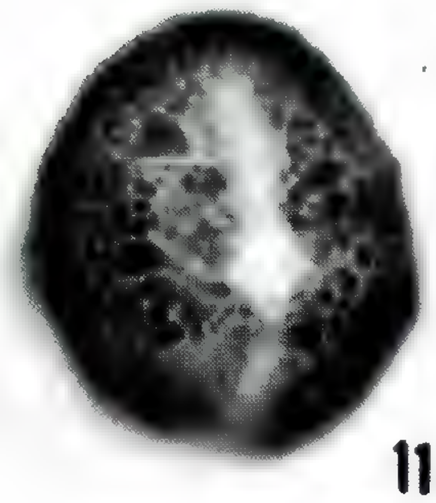
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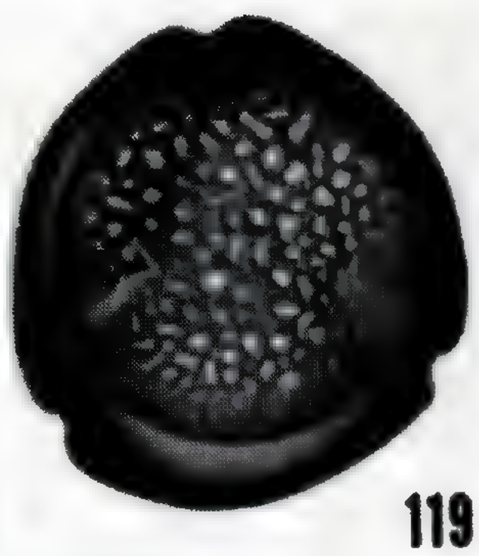
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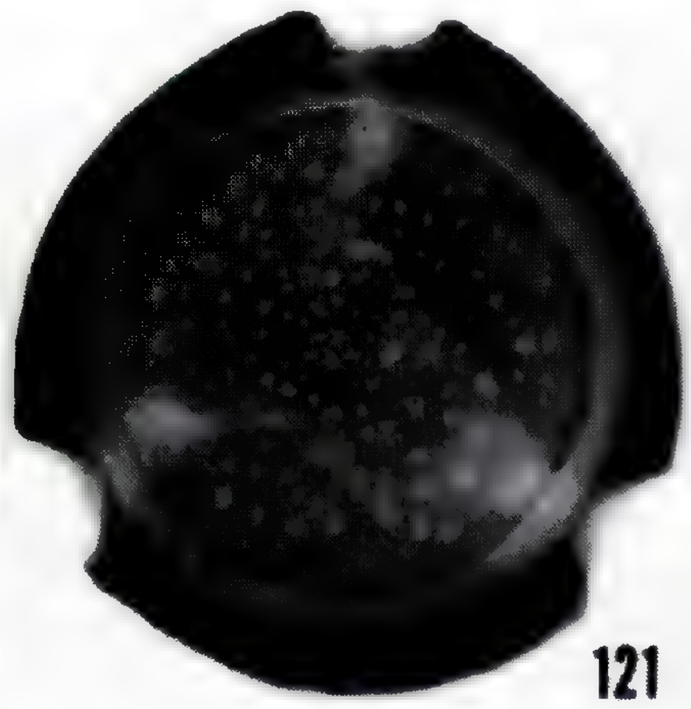
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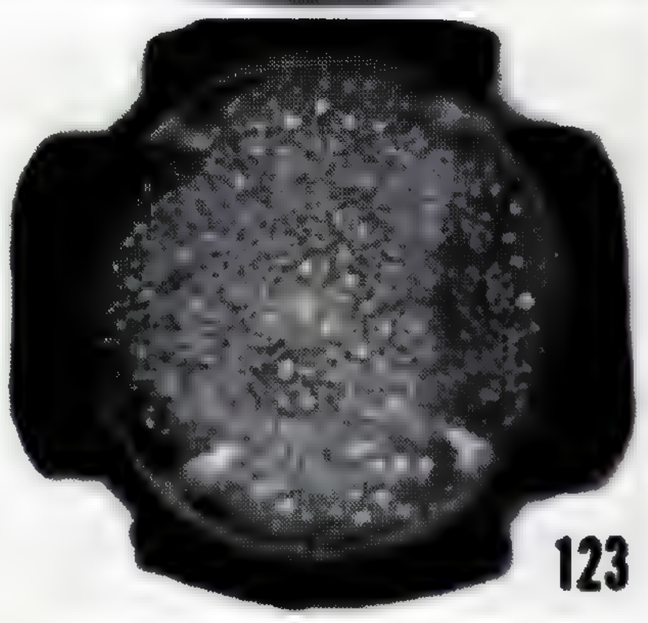
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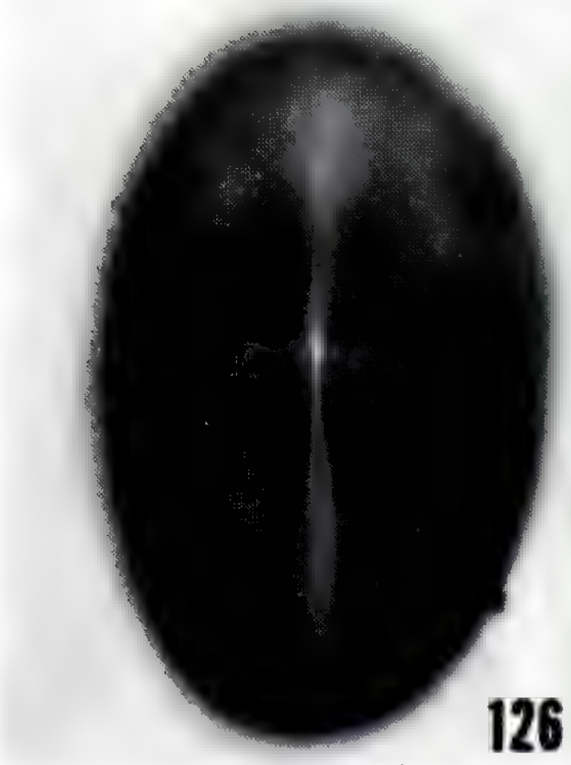
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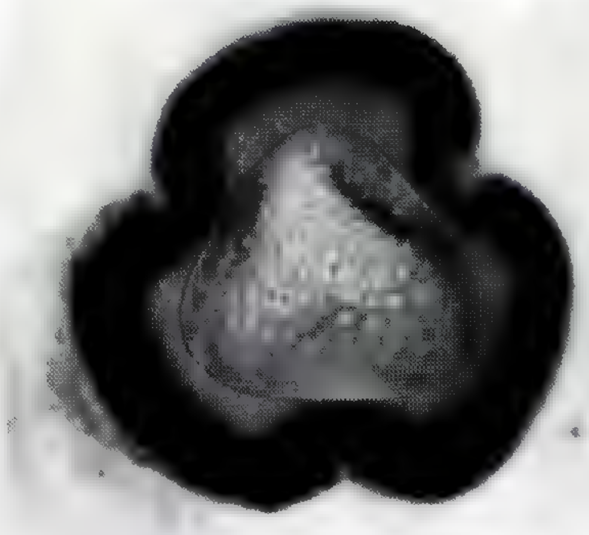
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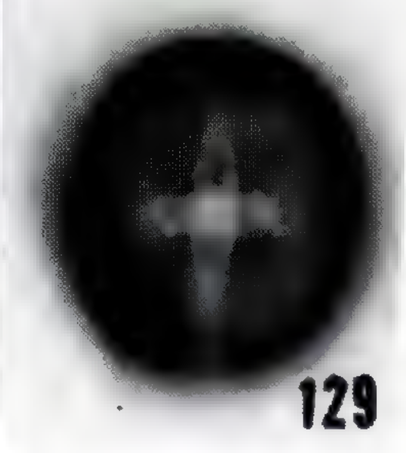
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FIGURES 116–130. Pollen of Flacourtiaceae, tribe Casearieae, × 1000.—116–118. *Gossypiospermum eriophorum* (*Jack 4970*).—116. Equatorial view with indeterminate colpus.—117. Equatorial view showing grain with verrucate-rugulate surface.—118. Polar view, optical cross section and polar surface of pentaperturate grain.—119. *Laetia procera* (*Ekman 12380*), polar view, optical cross section and reticulate polar surface.—120–121. *L. apetala* (*Hassler 7515*).—120. Equatorial view with colpus and pore.—121. Polar view, optical cross section

Idesia Maxim. Figs. 96–97.

Pollen grains prolate-spheroidal, semitectate, reticulate, lumen 1–2μ. Exine thickness 1.5μ. Tricolporoidate, costate, endoapertures often absent due to constricted colpi at equator. Average size: P = 23–28μ; E = 20–25μ.

Specimen examined: *I. polycarpa* Maxim.—China, *Forrest 17558* (US).

CASEARIEAE

Casearia Jacq. Figs. 98–115.

Pollen grains spheroidal to prolate, polar view circular to semiangular, semitectate to tectate, psilate to mostly reticulate or per-reticulate, lumen 0.3–4μ. Exine thickness 1–3μ. Tri(-4-)colporate, endoapertures equatorially elongate with pointed ends, costate. Average size: P = 18–58μ; E = 18–45μ.

Specimens examined: *C. aculeata* Jacq.—Mexico, *Rouirosa 568* (US). *C. aequilateralis* Merr.—China, *Lau 39* (US). *C. arborea* (L. C. Rich.) Urb.—Cuba, *Webster 4082* (US). *C. arguta* H. B. K.—Chile, *Sargent 27* (US). *C. bahamensis* Urb.—Cuba, *Britton, Cowell & Earle 10300* (US). *C. blanchetiana* Miq.—Peru, *Klug 2294* (US). *C. boliviana* Briq.—Bolivia, *Britton & Rusby 2421* (US). *C. cambessedesii* Eichl.—Columbia, *Haught 2828* (US). *C. celastroides* Kl.—British Guiana, *Smith 2449* (US). *C. cineria* Turcz.—Philippines, *Cabibe 5* (US). *C. comocladifolia* Vent.—Haiti, *Miller 276* (US). *C. corymbosa* H. B. K.—Columbia, *Dugand 6890* (US). *C. decandra* Jacq.—Puerto Rico, *Britton, Stevens & Hess 2387* (US). *C. dinklagei* Gilg—Liberia, *Cooper 408* (US). *C. disticha* A. Gray—Fiji, *Degener & Ordonez 23588* (US). *C. fasciculata* (R. & P.) Sleum.—Brazil, *Krukoff 6488* (US). *C. floribunda* (Mart.) Burret—Congo, *Gossweiler 718* (US). *C. fuliginosa* Blco.—Philippines, *Cuming 1240* (US). *C. grandiflora* Camb.—Brazil, *Ducke 80* (US). *C. graveolens* Dalz.—China, *Rock 2839* (US). *C. guianensis* (Aubl.) Urb.—Panama, *Paul 606* (US). *C. hirsuta* Sw.—West Indies, *Curtiss 310* (US). *C. hosei* Merr.—North Borneo, *Villamil 355* (US). *C. inaequilateria* Camb.—Brazil, *Smith & Reitz 9646* (US). *C. javitensis* H. B. K.—Brazil, *Killip & Smith 30153* (US). *C. nitida* Jacq.—Mexico, *Hinton 15803* (US). *C. obovata* Schlecht.—Mexico, *Matuda 4437* (US). *C. odorata* Macf.—Jamaica, *Harris 9808* (US). *C. ophiticola* M. Vict.—Cuba, *Figueiras 1261* (US). *C. pringlei* Briq.—Mexico, *McVaugh 10216* (US). *C. sylvestris* Sw.—Colombia, *Klug 1720* (US). Costa Rica, *Smith 1003* (US). *C. tomentosa* Roxb.—India, *Stewart 13756* (US).

Gossypiospermum Urb. Figs. 116–118.

Pollen grains prolate to prolate-spheroidal, semitectate, rugulate-reticulate, lumen 0.3μ. Exine thickness 1.3μ. Apertures 3, 4, 5-colporate in equal quantities, costate, colpi may be branched often with ragged edges and indeterminate ends; often very diffuse. Average size: P = 28–33μ; E = 23–28μ.

Specimen examined: *G. eriophorum* (C. Wr.) Urb.—Cuba, *Jack 4970* (US).

Laetia Loefl. *ex* L. Figs. 119–123.

Pollen grains subprolate, tectate, reticulate to occasionally rugulate, lumen

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and polar surface of semitectate grain.—122–123. *L. thamnia* (*Lundell 7430*).—122. Equatorial view with colpus and pore surrounded by a rugulate exine.—123. Polar view, optical cross section and semitectate polar surface.—124–125. *Hecatostemon quazumiifolius* (*Smith 174*).—124. Equatorial view.—125. Polar view, optical cross section and reticulate polar surface.—126. *Ryania speciosia* (*Cuatrecasas 6847*), equatorial view with colpus and pore.—127–128. *R. canescens* (*Prance, Silva & Pires 59148*).—127. Equatorial view, colpus and pore.—128. Polar view, optical cross section and polar surface.—129–130. *Zuelania roussovieae* (*Purpus 10703*).—129. Equatorial view, colpus and pore.—130. Polar view, optical cross section and polar surface.

1–4μ. Exine thickness 1.3–2.3μ. Apertures 3, 4-colporate, costate, ends of colpi often indeterminate, ends diffuse. Average size. P = 25–40μ; E = 25–35μ.

Specimens examined: *L. apetala* Jacq.—Paraquay, *Hassler 7515* (US). *L. procera* (Poepp. & Endl.) Endl.—Hispaniola, *Ekman 12380* (US). *L. suaveolens* (P. & E.) Bth.—Peru, *Klug 1443* (US). *L. thamnia* L.—Mexico, *Lundell 7430* (US).

Hecatostemon Blake Figs. 124–125, 171–172.

Pollen grains prolate-spheroidal, semitectate, reticulate, duplibaculate, lumen 1–3μ. Exine thickness 2μ. Tricolporate, costate, endoapertures equatorially elongate, ends diffuse. Grains often appearing anisopolar due to proliferations of ektexine over colpi membranes on one side of ora. Average size: P = 35–42μ; E = 30–38μ.

Specimens examined: *H. guazumifolius* (H. B. K.) Sleum.—Venezuela, *Smith 174* (US).

Ryania Vahl Figs. 126–128.

Pollen grains prolate, tectate, reticulate, simplibaculate, lumen 0.3–1μ. Exine thickness 2μ. Tricolporate, endoapertures equatorially elongate. Average size: P = 35–48μ; E = 23–33μ.

Specimens examined: *R. angustifolia* (Turcz.) Monach.—Brazil, *Holt & Gehringer 380* (US). *R. canescens* Eichl.—Brazil, *Prance, Silva & Pires 59148* (US). *R. speciosa* var. *chocoensis* (Tr. & Pl.) Monach.—Columbia, *Cuatrecasas 6847* (US).

Zuelania A. Rich. Figs. 129–132.

Pollen grains prolate, tectate, finely reticulate or psilate, lumen 0.3μ or absent. Exine thickness 1.5–2μ. Apertures 3, 4-colporate, costate, endoapertures equatorially elongate. Average size: P = 28–38μ; E = 28–35μ.

Specimens examined: *Z. guidonia* (Sw.) Britton & Millsp.—Mexico, *Purpus 10703* (US), *Enriquez 567* (US).

Osmelia Thwaites Figs. 133–134.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1–1.5μ. Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: P = 20–33μ; E = 13–23μ.

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FIGURES 131–150. Pollen of Flacourtiaceae, tribe Casearieae, × 1000.—131–132. *Zuelania guidonia* (*Enriquez 567*).—131. Equatorial view, colpus and pore.—132. Polar view, optical cross section and polar surface.—133–134. *Osmelia bartlettii* (*Krukoff 4003*).—133. Equatorial view, colpus and pore.—134. Polar view, optical cross section and polar surface.—135–136. *Ophiobotrys zenkeri* (*Vique 1753*).—135. Equatorial view.—136. Polar view, optical cross section and polar surface.—137–138. *Lunania mexicana* (*Purpus 7776*).—137. Equatorial view, colpus and pore.—138. Polar view, optical cross section and polar surface.—139–140. *Euceraea nitida* (*Fernandez s. n.*).—139. Equatorial view, colpus and pore.—140. Polar view, optical cross section and polar surface.—141–142. *Tetrathylacium macrophyllum* (*Woytkowski 7634*).—141. Equatorial view.—142. Polar view, optical cross section and polar surface.—143–145. *Samyda yucatanensis* (*Lundell 7338*).—143. Equatorial view, reduced aperture.—144. Polar view, optical cross section and polar surface.—145. Equatorial view of aperture, shortened colpus and lalongate pore.—146–148. *Neoptychocarpus apodanthus* (*Ducke 1633*).—146. Equatorial view of colpus and margin.—147. Equatorial view, internal surface of pore.—148. Polar view, optical cross section and reticulate, simplibaculate polar surface.—149–150. *Samyda dodecandra* (*Sargent 652*).—149. Equatorial view, colpus.—150. Polar view, optical cross section and polar surface.

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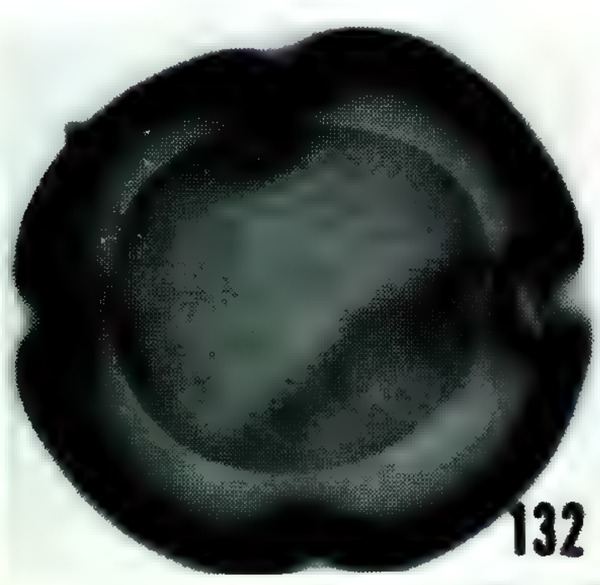
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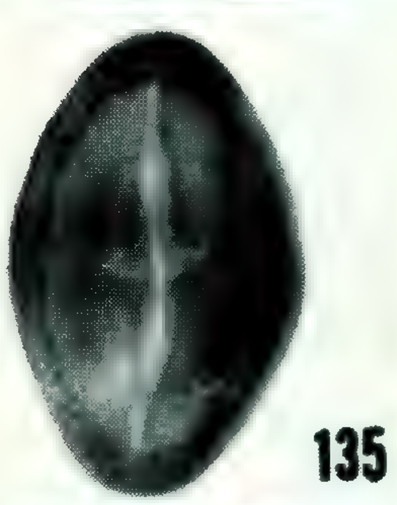
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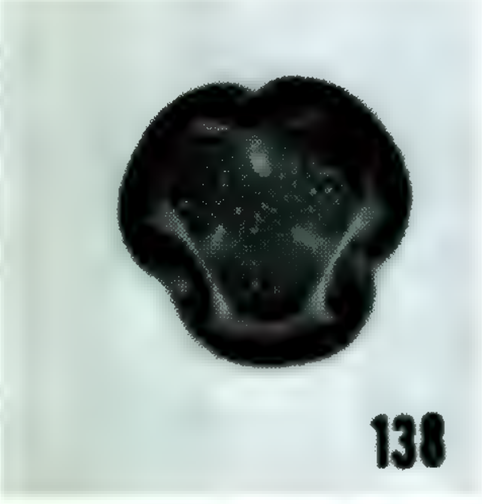
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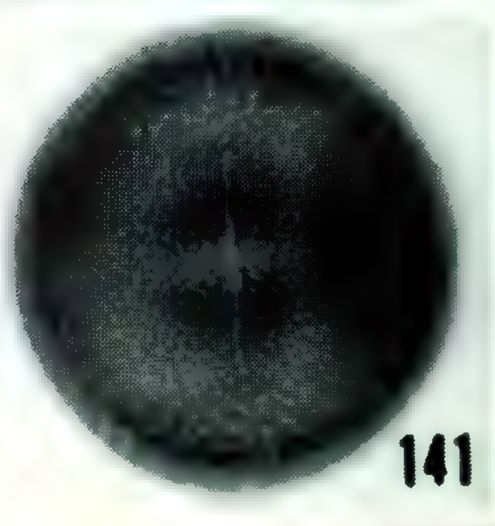
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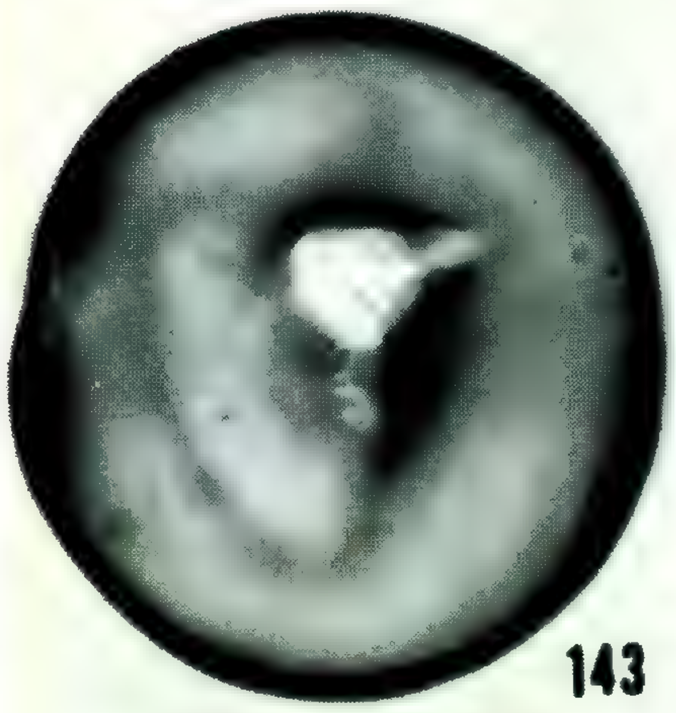
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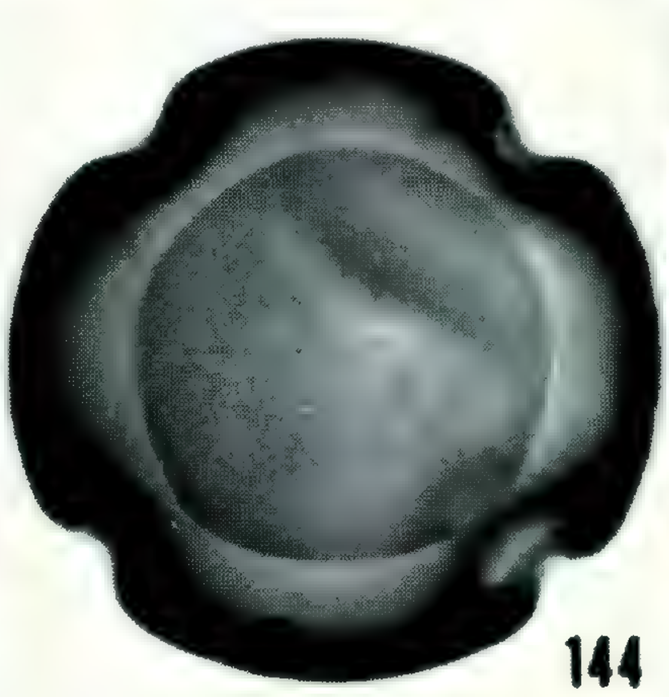
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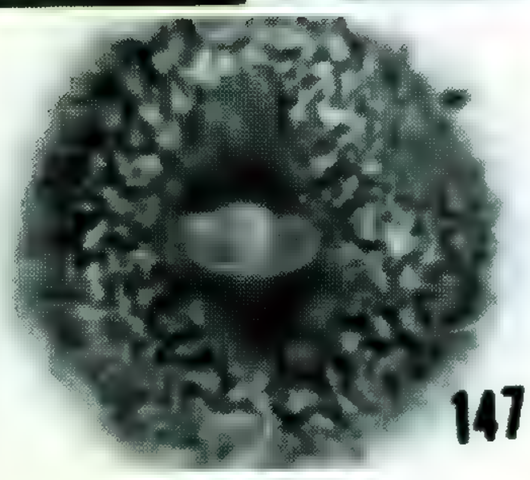
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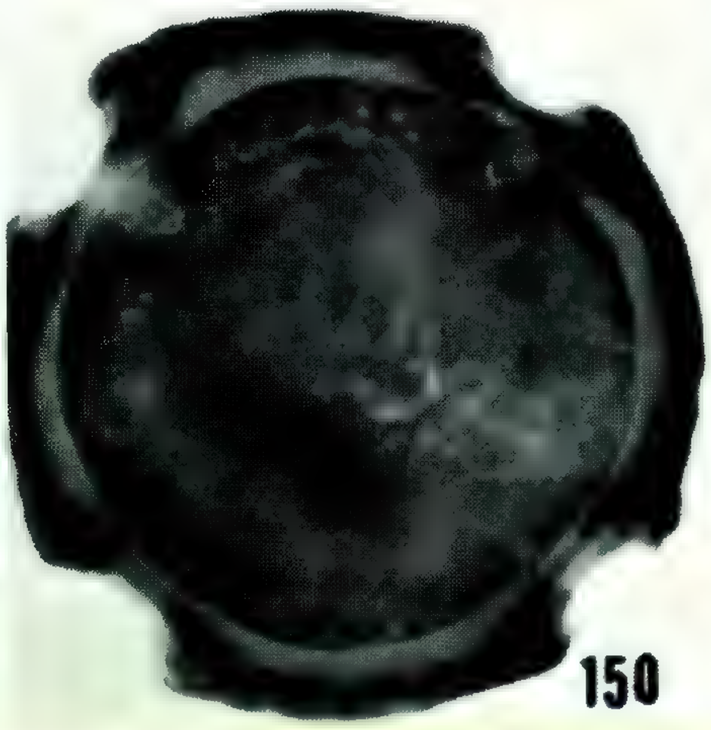
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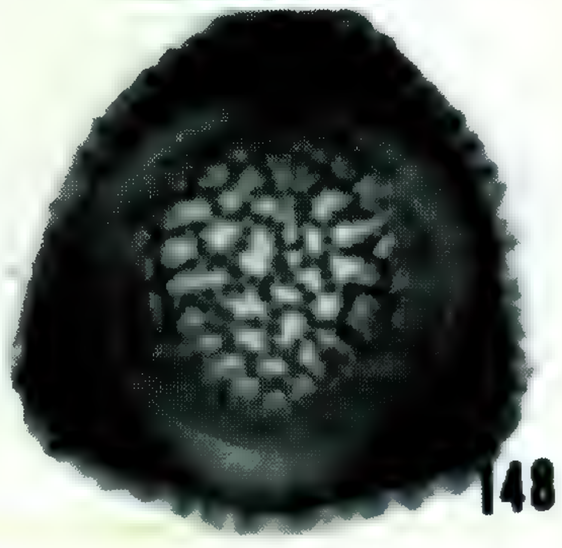
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Specimens examined: *O. bartlettii* Merr.—Sumatra, *Krukoff 4003* (US). *O. maingayi* King—Malaya, *Kochummes 75982* (US). *O. philippinensis* Benth.—Philippines, *Ahern 133* (US).

Ophiobotrys Gilg Figs. 135–136.

Pollen grains prolate, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1.5–2μ. Tricolporate, costate, endoapertures equatorially elongate, often with pointed ends. Occasional ektexine elements above endoapertures on colpi membranes. Average size: P = 28–30μ; E = 18–20μ.

Specimen examined: *O. zenkeri* Gilg—Ghana, *Vique 1753* (US).

Lunania Hook. Figs. 137–138.

Pollen grains prolate, tectate, reticulate, lumen 1–3μ. Exine thickness 1.5μ. Tricolporate, costate, endoapertures equatorially elongate with blunt or usually pointed ends. Average size: P = 18–25μ; E = 13–18μ.

Specimens examined: *L. mexicana* Brandeg.—Mexico, *Purpus 7776* (US). *L. parviflora* Spruce *ex* Benth.—Peru, *Wurdack 1820* (US), *Vargas 17785* (US).

Euceraea Mart. Figs. 139–140.

Pollen grains are prolate, tectate, reticulate, simplibaculate, lumen 1μ. Exine thickness 1μ. Tricolporate, costate, endoapertures equatorially elongate, oval. Average size: P = 30–33μ; E = 23–25μ.

Specimen examined: *E. nitida* Mart.—Colombia, *Fernandez s. n.* (US).

Tetrathylacium Poepp & Endl. Figs. 141–142.

Pollen grains spheroidal, semitectate, reticulate to verrucate, lumen 0.5μ. Exine thickness 1–2.5μ. Tricolporate, costate, colpi short, narrow, endoapertures equatorially elongate with blunt, indeterminate ends. Average size: P = 20–28μ; E = 20–25μ.

Specimens examined: *T. costaricense* Stand.—Costa Rica, *Skutch 4281* (US). *T. macrophyllum* P. & E.—Peru, *Woytkowski 7634* (US).

Samyda Jacq. Figs. 143–145, 149–150.

Pollen grains prolate-spheroidal, tectate, reticulate to rugulate, lumen 0.3–0.7μ. Exine thickness 1.5–2μ. Apertures 4, 5-colporate, costate, placement of apertures often irregular, off the equator and diagonal to the meridian. Colpi often reduced or fragmented. Endoapertures elliptical meridianally with constricted pointed ends, equatorially elongate extensions give a cross shape to the endoaperture. Some ektexine elements on colpi membranes. Average size: P = 30–40μ; E = 30–40μ.

Specimens examined: *S. dodecandra* Jacq.—Puerto Rico, *Sargent 652* (US). *S. yucatanensis* Standl.—Mexico, *Lundell 7338* (US).

Neoptychocarpus Buchheim Figs. 146–148.

Pollen grains spheroidal or prolate spheroidal, semiangulaperturate in polar view, semitectate, per-reticulate, simplibaculate, lumen 4–5μ. Exine thickness 2.5μ. Tricolporate, costate, endoapertures equatorially elongate and elliptical. Average size: P = 28–30μ; E = 28–30μ.

Specimen examined: *N. apodanthus* (Kuhl.) Buchheim—Brazil, *Ducke 1633* (US).

Abatia Ruiz & Pavon Figs. 151–156.

Pollen grains prolate to prolate-spheroidal, tectate, finely reticulate, lumen 0.5μ. Exine thickness 1.5–2μ. Tricolporate, endoapertures equatorially elongate, costate, ektexine elements occasionally on the colpi membranes above and below endoapertures. Average size: P = 18–30μ; E = 15–30μ.

Specimens examined: *A. borealis* L. O. Wms.—Costa Rica, *Lankester 674* (US). *A. parviflora* R. & P.—Colombia, *Fosberg & Villareal 20577* (US). *A. spicata* (Turcz.) Sleum.—Peru, *Bingham 2067* (US). *A. tomentosa* Mart.—Brazil, *Barreto 19905* (US).

Aphaerema Miers Figs. 157–158.

Pollen grains prolate, tectate, finely reticulate, lumen 0.3μ. Exine thickness 1.5μ. Tricolporate, costate, endoapertures equatorially elongate with pointed ends. Average size: P = 18–20μ; E = 15–18μ.

Specimen examined: *A. spicata* Miers—Brazil, *Klein 444* (US).

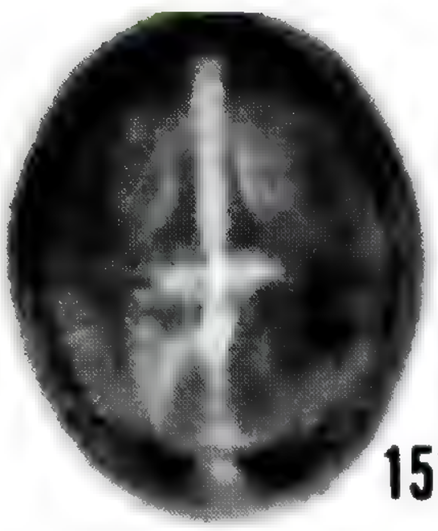
Level of Advancement

Traditionally, comparative morphologists state that the only trend of specialization anchored in the fossil record is that of tracheary tissue. Recent pollen analysis from carefully dated Mesozoic and Cenozoic strata, however, have added another order of precision to our knowledge of evolutionary specialization of the angiosperms (Brenner, 1967; Doyle, 1969; Muller, 1970).

In schemes depicting the earliest evolution of dicotyledonous pollen, trizoniaperturate pollen is considered relatively specialized (Muller, 1970; Kuprianova, 1967, 1969; Nair, 1965). However, in surveys of the complete range of modern dicotyledonous pollen types, the small, reticulate, tricolpate and tricolporate types form the basis for considerable further specialization and elaboration. This kind of pollen is represented in Cenomanian strata (Brenner, 1967).

In his study of the Cretaceous pollen record of the Atlantic coast, Doyle (1969) found a statistical trend in the triaperturate type which included tricolpate, tricolporoidate, tricolporate and triporate pollen in successively higher levels. The earliest grains were prolate or subspheroidal, retipilate or reticulate, occurred as single grains, and were small in size. In the evolution of the triaperturate type, many genera of Flacourtiaceae are primitive in all criteria.

While the affinities of these early pollen types are uncertain, it has been suggested that grains of Polycarpiciae, Amentiferae and Cistiflorae are represented (Muller, 1970). Specialized trends as found in the Theales make the identification of those pollen types from early strata less tentative. Many early Cretaceous pollen grains have been assigned to Dilleniaceae, Ochnaceae, Salicaceae, and Columniferae. Despite the fact that pollen of many extant genera of Flacourtiaceae are indistinguishable from pollen occurring in the above mentioned families, the earliest pollen assigned to the Flacourtiaceae is from the upper Miocene (Muller, 1970). It seems probable that earlier pollen of Flacourtiaceae has been misidentified due to lack of knowledge of the family. Previous statistical correlations between vegetative and floral features have placed the Flacourtiaceae among the most primitive of angiosperm families (Sporne, 1954).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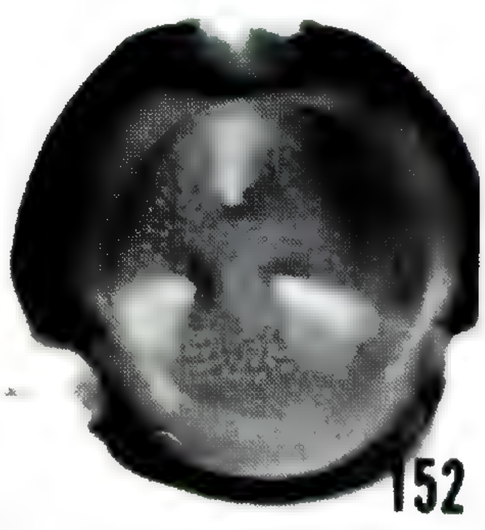
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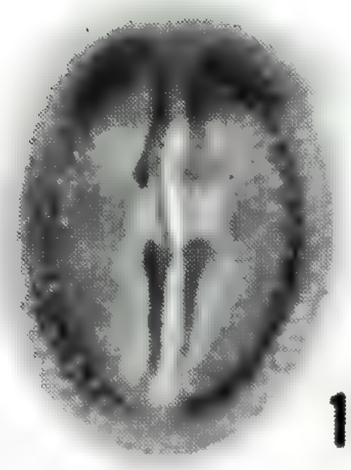
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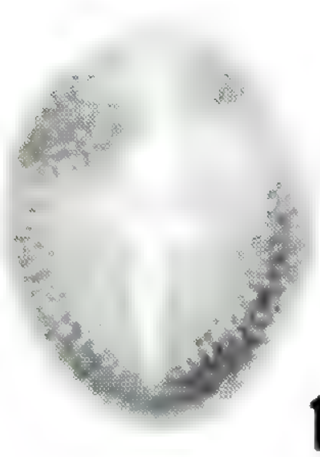
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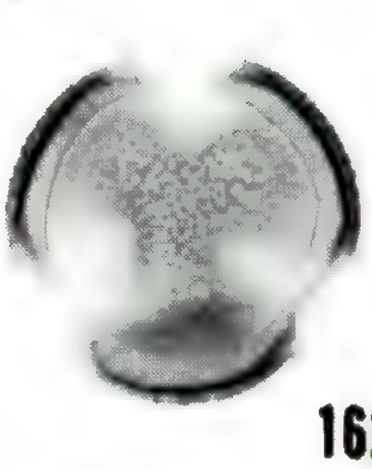
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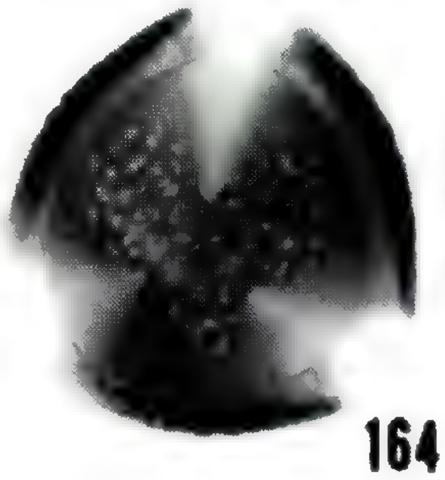
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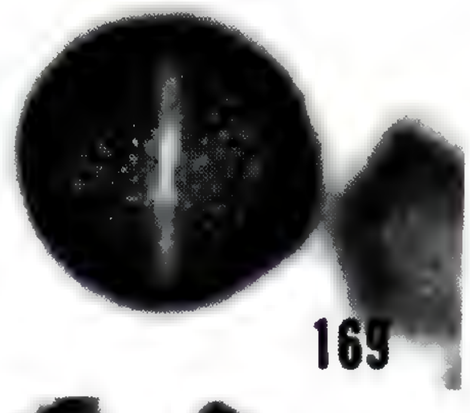
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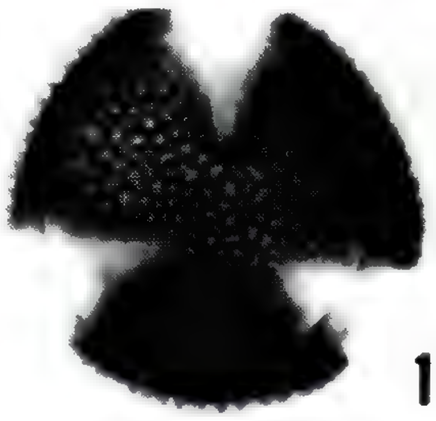
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FIGURES 151–170. Pollen of Flacourtiaceae and certain excluded genera, tribes Casearieae, Prockieae, and Paropsieae, × 1000.—151–158. Casearieae.—151–152. *Abatia borealis* (*Lankester 674*).—151. Equatorial view.—152. Polar view, optical cross section and polar surface.—153–154. *A. parviflora* (*Fosburg & Villareal 20577*).—153. Equatorial view.—154.

Many genera of Flacourtiaceae have pollen that conform to the criteria of wind pollination as defined by Whitehead (1969). These include production and release of numerous grains, exposed anthers and stigmas, grain diameter 20–40μ, thin exines and a smooth surface. Considerably more observations are needed in this family before the relation between pollen morphology and mechanisms of pollination can be adequately discussed. Detailed studies of the records of several families indicate that pollen evolution is concurrent with taxonomic diversification (Muller, 1970). This should prove to be the case in the Flacourtiaceae.

Summary of Intrafamilial Relationships

The tribes Berberidopsideae and Oncobeae do not appear sharply defined from each other. While the grains of the Berberidopsideae are small to medium-sized, some of the largest grains in the family are found in *Mayna* and *Carpotroche* of the Oncobeae. Both tribes have a tendency toward high, equatorially elongate, rectangular endoapertures. The tricolpate pollen of *Berberidopsis* is the most primitive of the family.

Sculpturing varies in these tribes from psilate to coarsely reticulate. Some treatments of the family (Bamps, 1968; Gilg, 1925) do not separate the two tribes, leaving all genera in the Oncobeae. The limited pollen sample of this study, while diverse, does not clearly show a separation along tribal lines as suggested by Hutchinson (1967).

The tribes Scolopieae, Banareae, Homalieae, and Flacourtieae have pollen which can scarcely be distinguished. The tribe Prockieae, assigned by Hutchinson to the Tiliaceae, could easily be added to this group. All have costate colpi, a wide or narrow endoaperture, and a reticulate or finely reticulate exine. Costae in the Homalieae tend to be abbreviated. In *Homalium* and *Dissomeria*, the costae are concentrated at the four corners of the intersection formed by the endo- and ecto-apertures. In some *Homalium* specimens, the costae only define the margins of the endoapertures. It is doubtful if keys to the pollen of most of these genera could be made without electron microscope preparations of the wall. One specimen labelled *Banara costaricensis* (Standl.) Sleumer (Figs. 44–45) is about twice as large as any other known *Banara* specimen. In aperture morphology and sculpturing, it most closely resembles pollen of the genus *Casearia*.

←

Polar view, optical cross section and polar surface.—155–156. *A. spicata* (*Bingham 2067*).—155. Equatorial view.—156. Polar view, optical cross section and polar surface.—157–158. *Aphaerema spicata* (*Klein 444*).—157. Equatorial view.—158. Polar view, optical cross section and polar surface.—159–162. Prockieae.—159–160. *Hasseltia lateriflora* (*Smith 1915*).—159. Equatorial view.—160. Polar view, optical cross section and polar surface.—161–162. *Prockia crucis* (*Hinton 4277*).—161. Equatorial view.—162. Polar view, optical cross section and polar surface.—163–170. Paropsieae.—163–164. *Soyauxia floribunda* (*Straub 107*).—163. Equatorial view.—164. Polar view, optical cross section and reticulate polar surface.—165–166. *Smeathmannia pubescens* (*Straub 117*).—165. Equatorial view.—166. Polar view, reticulate, hexacolpate grain.—167–168. *Paropsiopsis pulchra* (*Zenker 413*).—167. Equatorial view, pair of colporate apertures.—168. Polar view, optical cross section and polar surface of hexacolpate grain.—169–170. *Ancistrothyrsis tessmannii* (*Ducke 24387*).—169. Equatorial view.—170. Polar view, optical cross section and reticulate polar surface.

Some of the genera of Casearieae resemble the previous group of four tribes but add more specialized trends. These include greater size, more frequent 4–5 aperturate grains, and wide elongate endoapertures with pointed ends (*Casearia*). Some per-reticulate grains (*Neoptychocarpus*) and breviaperturate grains (*Samyda*) are also found. Thicker, unsculptured and unstructured exines are found in *Casearia*.

The Pangieae are isolated and have a number of different specialized features in different genera. Among these are brevicolpate to porate apertures (*Pangium*, *Ryparosa*), large grains with per-reticulate sculpturing (*Hydnocarpus*), rugulate sculpturing (*Trichadenia*), thick, conspicuously costate exines (*Kiggelaria*), and medium to large size in all specimens examined.

The Paropsieae are as isolated from the other tribes in their pollen morphology as are the Pangieae. Their sculpturing pattern is per-reticulate of the simplibaculate type and is separable from the other tribes on this appearance. This sculpturing pattern most closely resembles the per-reticulate type of the Passifloraceae rather than the perforated tectum, duplibaculate type found in the Oncobeae (*Mayna*). The hexacolporate, paired apertures especially separate this tribe from other Flacourtiaceae.

INTERFAMILIAL RELATIONSHIPS

Although pollen provides but one set of characters which must be correlated with observations on other structures before intrageneric and familial relationships will be resolved, it remains useful to comment on the degree of resemblance of pollen of various families to that of the Flacourtiaceae. Families from eleven orders are thought to be related to a flacourtiaceous stock (Takhtajan, 1969). In the following comparison, Takhtajan's (1969) organization will be followed. Unless otherwise acknowledged, comparative pollen data is from Erdtman (1952).

Violales.—The Lacistemaceae and Stachyuraceae have been considered quite close to the Flacourtiaceae. The pollen morphology is quite supportive of this arrangement, the grains being small to medium-sized, finely reticulate, tricolporate and with equatorially elongate endoapertures.

The Violaceae are considered by Takhtajan (1969) to be linked to the Flacourtiaceae through the primitive tribe Rinoreeae. Some pollen of this family is well within the range of the Flacourtiaceae, but other tribes show increased specialization. This includes large size, up to five apertures, and protruding aperture margins.

The Bixaceae and Cochlospermaceae, considered related in most schemes, have pollen which allows separation of the two families and separation from the Flacourtiaceae (Keating, 1972; Nair, 1962*a*). Their pollen fits the range of the Flacourtiaceae, especially resembling the tribe Oncobeae. However, cochlospermaceous and bixaceous pollen is distinct enough to make any tribal alliance uncertain. The Cistaceae have pollen quite similar to that of the Flacourtiaceae. The endoapertures are oval or circular. More specialized tendencies include larger size, striate grains, and a more complex reticulum (Heydacker, 1963; Jean & Pons, 1963).

On the basis of pollen the Violales seem to be a related group of families with the Flacourtiaceae as basic for this assemblage.

Passiflorales.—The Passifloraceae have long been considered closely allied to the Flacourtiaceae through the tribe Paropsieae (see review by DeWilde, 1971). Gilg (1925) considered the Paropsieae to be Tribe III of the Flacourtiaceae, but on the basis of pollen it forms an isolated group in the family. Pollen morphology of the tribe has been described by Spirlet (1965) and Presting (1965) with the finding that the genera agree quite closely with other Passifloraceae. Pollen of the Passifloraceae can be tricolporate, but many genera are distinctly six and twelve zonicolporate. *Paropsiopsis* (Figs. 167–168) and *Smeathmannia* (Figs. 165–166) illustrate another characteristic feature of some Passifloraceae, especially of *Passiflora*, the tendency for multiple apertures to be grouped in pairs. This highly distinctive pattern seems unquestionably to belong in the Passifloraceae. Pollen of the genera *Ancistrothyrsis* (Figs. 169–170) and *Soyauxia* (Figs. 163–164) are only tricolporate and closer to the Flacourtiaceae.

When included in the Flacourtiaceae, the tribe is distinguished by the presence of a corona; in the Passifloraceae, the tribe is distinguished by its arboreous habit (DeWilde, 1971). The evidence from pollen supports the concensus of intermediacy of the tribe, but its best placement seems to be with the Passifloraceae (Sleumer, 1970; DeWilde, 1971).

The remaining families of the Passiflorales (Turneraceae, Malesherbiaceae, Achariaceae, and Caricaceae) seem derived from the Passifloraceae on the basis of pollen and more distantly related to the Flacourtiaceae. Their pollen grains are tricolporate, tend to be of large size, and often have more complex sculpturing patterns.

Cucurbitales.—The Cucurbitaceae, considered derived from the Passifloraceae (Takhtajan, 1969), show more highly evolved pollen than the Passifloraceae (Jeffrey, 1964; Awasthi, 1962*a*, *b*; Saad, 1964; Marticorena, 1963). Pollen of several tribes in the subfamily Cucurbitoideae (Jeffrey, 1964) are similar to flacourtiaceous pollen. Pollen of the tribes Joliffieae, Melothrieae, Schizopeponeae and of the subfamily Zanonioideae are tricolporate, small, prolate, and finely reticulate. An equatorially elongate endoaperture is often present. More highly evolved types are found in the remaining tribes which include 4–10 apertures, pantoporate, and spinose grains. Clearly, pollen provides data compatible with the systematic position of the family.

Salicales.—Persistant suggestions have related the Salicaceae to the Flacourtiaceae, especially to Flacourtieae (Hutchinson, 1967) or Idesiinae (Gilg, 1925). Pollen of *Salix* is tricolporoidate or tricolporate with a reticulate sculpture and size (Risch, 1960) that is quite similar to that found in *Idesia* or *Itoa*. Pollen of *Populus* is inaperturate and derived. The data of Nair (1967) on pollen of Monochlamydeae, while not explicit on this relationship, is compatible with this scheme. Rowley and Erdtman (1967) have provided structural data by electron microscopy which will be of value for comparisons of similar studies of Idesiineae.

Begoniales.—The Begoniaceae and Datiscaceae produce pollen grains with some features similar to pollen of Flacourtiaceae. They are small, spheroidal to

perprolate and have an obscure sculpture. They differ in the presence of a striate pattern, having endoapertures with granulate membranes and occasionally being shed as tetrads. This group may be derived from Violales but is more distantly related.

Capparales.—Pollen of Capparaceae, while similar in some ways to the Flacourtiaceae, has evolved a thicker and more complicated reticulate exine with small spines.

Tamaricales.—The Tamaricaceae and Frankeniaceae have pollen which does not resemble that of the Flacourtiaceae. The grains are 2, 3, 4-colpate and may have granulate colpi membranes.

Malvales.—The Elaeocarpaceae have small, tricolporoid, prolate pollen quite similar to the Homalieae type within the Flacourtiaceae. With their finely reticulate pattern, these grains would not be readily distinguishable.

While pollen of the Tiliaceae is quite variable, that of the *Grewia* type is quite similar to flacourtiaceous pollen. It is not very different from the genus *Kiggelaria* (Chaudhuri & Mallik, 1965; Erdtman, 1952). Pollen of *Heritiera* is also quite similar to the Flacourtiaceae. The morphology of the compound apertures and of the exine is similar to that found in the Flacourtiaceae (Tarnavschi & Şerbănescu-Jitariu, 1968).

Pollen of the Sterculiaceae even more closely resembles that of the Flacourtiaceae. The tribe Sterculieae shows the closest pattern, especially the equatorially elongate endoapertures and the finely reticulate exine (Litchfield, 1966; Rao, 1950; Erdtman, 1964). (E.g. *Brachychiton* and *Argyrodendron* would fit easily among flacourtiaceous pollen.) Of the other tribes, pollen of the Buttnerieae is also not very different.

The tribe Prockieae, including the genera *Hasseltia* (Figs. 159–160), *Prockia* (Figs. 161–162), and *Neosprucia*, was removed from the Flacourtiaceae by Hutchinson (1959) and placed in the Tiliaceae. On the basis of pollen morphology, there is no support for the removal of these genera. They fit perfectly well among the Banarieae.

Among the Tiliaceae and Sterculiaceae are many genera showing highly evolved pollen including spininess, triangular shape, and elaborate porate apertures. Nevertheless, among the less specialized members of these families, a definite affinity can be found with the Flacourtiaceae. The pollen of these two families can be considered as a type distinct from malvaceous or bombacaceous pollen (Chaudhuri & Mallik, 1965).

Pollen grains of the Rhopalocarpaceae are medium to large, 3–6-colpate, colporate, and oblate. The exine is echinate or subechinate. In the past this group has been placed in the Violales (with the Cochlospermaceae), the Theales or Malvales, but recent studies by Huard (1965*a*, *b*) confirm their placement in the Malvales. They are not close to the Flacourtiaceae.

The Bombacaceae have pollen which are quite different from the Flacourtiaceae. Advanced trends include highly spinose, per-reticulate rugulate or verrucate exines, fossaperturate shape, or elaborate aperture patterns. (Tsukada, 1964; Fuchs, 1967; Robyns, 1963; Nair, 1962b).

Malvaceae have mostly large, spinose pollen with thick walls and large

apertures. Many are panporate. Pollen of this family has the least similarity to the Flacourtiaceae of all of the malvalian families (Prasad, 1963; Sharma & Rastogi, 1965; Bronckers & Horvat, 1963; Saad, 1960; Nair, 1962*b*; Chaudhuri & Mallik, 1965).

Euphorbiales.—The Euphorbiaceae have features in common with both primitive Violales and Malvales and may have arisen from an ancestral group between them (Takhtajan, 1969). Pollen of the subfamily Phyllanthoideae (Punt, 1967), especially that of the *Antidesma* and *Richeria* types (Punt, 1962), is quite similar to flacourtiaceous pollen. The grains tend to be prolate, costate, small- to medium-sized, have equatorially elongate apertures with diffuse ends, and are reticulate or psilate-tectate. Other genera are more specialized in being verrucate, per-reticulate, fossaperturate, spinose or suprabaculate, and have to 4–5 apertures. Some genera are stephanocolpate, -porate, or inaperturate. The subfamily Crotonoideae is considerably more specialized.

This large, diverse family may well have had its origins in the Violales. On the other hand, Chaudhuri and Mallik (1965) have pointed out an apparent affinity between the Sterculiaceae and Phyllanthoideae, because of resemblances in the tricolporate, spheroidal-oblate pollen of some genera.

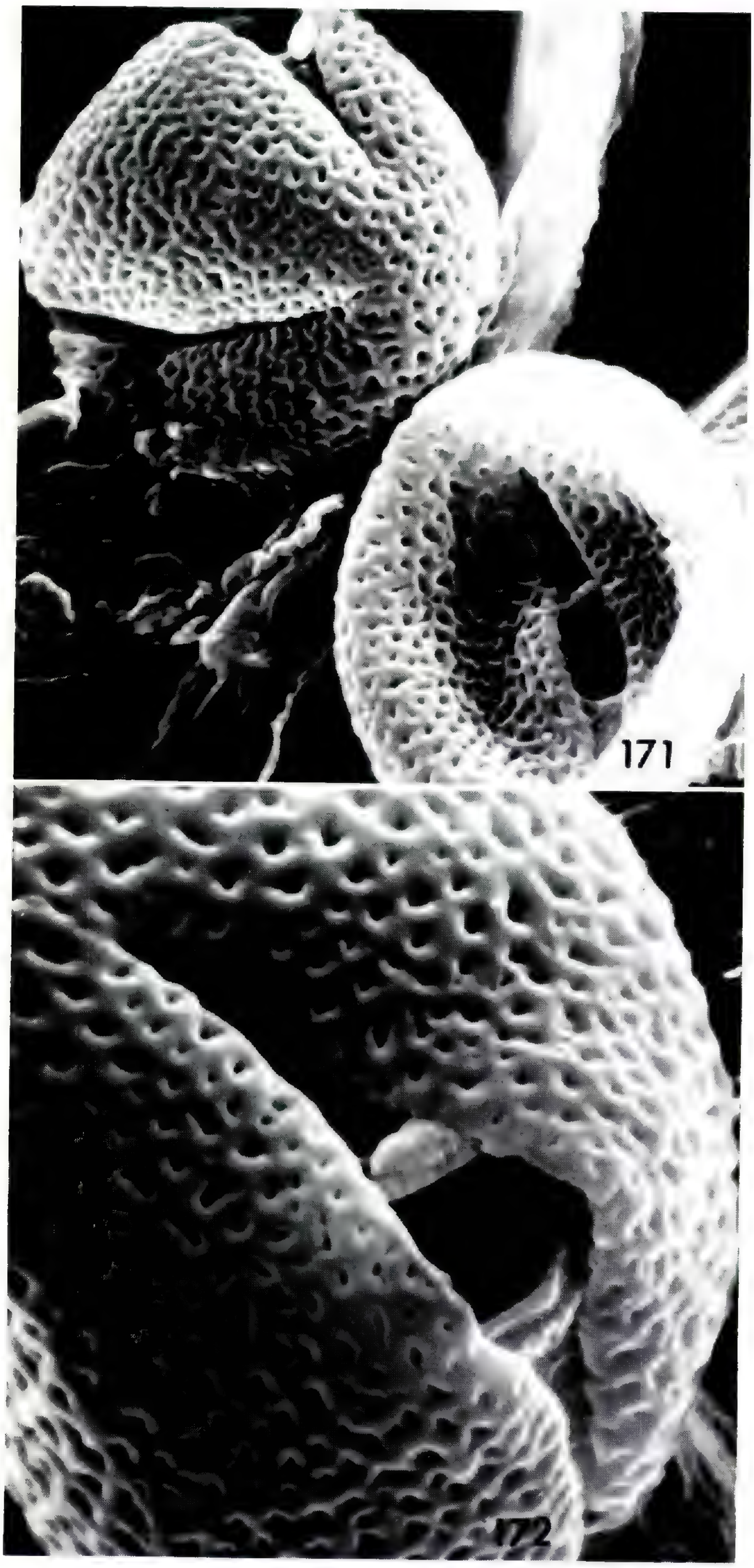
Dilleniales.—Studies by Dickison (1967), have shown the Dilleniaceae to have a variety of morphological types but, as with the Flacourtiaceae, the tribes cannot be delineated easily by pollen morphology. Dickison concluded that the Dilleniaceae show more resemblance to the Theales than to the Ranalian families. Violales were not considered closely related.

Direct comparisons in the present study show that the pollen of the Flacourtiaceae is quite compatible with that of the Dilleniaceae. Agreement includes the prolate to spheroidal shape, circular polar outline, small to medium size, tectate or semi-tectate structure, and finely reticulate to reticulate sculpture. Costae seem to be present but are not mentioned in Dickison's study. The compound apertures are somewhat different. The furrows are said to be provided with an operculum and often a margo. Trends toward four apertures and porate grains are paralleled in the Flacourtiaceae. It seems quite feasible to consider the Dilleniaceae a primitive connecting link between the Violales and Theales as stated by Takhtajan (1969).

Theales.—The Ochnaceae, a basal group in the Theales, have pollen which bears a strong resemblance to the Flacourtiaceae. The tricolporate, prolate, costate grains have an equatorially elongate endoaperture which is quite similar to the Flacourtiaceae. The ektexine is smooth, subverrucate, to finely reticulate (Muller, 1969). There is also an unmistakable resemblance to several higher families of Violales (Cochlospermaceae, Bixaceae, and Cistaceae).

Pollen of the Theaceae shows some similarities to flacourtiaceous pollen in size, shape, reticulate exine, equatorially elongate endoapertures, smooth colpi membranes, and costate margins. Some genera differ in having densely spaced pila, a spinuliferous ektexine, and granulate aperture membranes. The overall resemblance here is not as close as with the Ochnaceae.

The Clusiaceae (Guttiferae) and Hypericaceae have pollen with tendencies toward greater size, 4–5 apertures in an angulaperturate condition, and more



FIGURES 171–172. Pollen of Flacourtiaceae, tribe Casearieae, *Hecatostemon guazumiifolius* (*Smith 174*). Scanning electron photomicrographs of acetolyzed grains.—171. Oblique polar view and equatorial view of collapsed grain. ×2400. Note reticulate surface.—172. View of aperture. ×5900. Note equatorially elongate endoaperture disappearing from view beyond the edge of the colpus. An ektexine proliferation is visible extending along one side of endoaperture. It appears to originate on one side of the colpus margin. This ektexinal proliferation is also visible in both grains of Fig. 171.

highly specialized sculpture. A few species are tricolporate and finely reticulate. The equatorially elongate endoaperture is similar to the Flacourtiaceae.

Of the Theales, flacourtiaceous pollen most clearly resembles that of the Ochnaceae with the Theaceae, Clusiaceae, and Hypericaceae showing generally more highly evolved pollen.

It must be kept in mind that comparisons of the Flacourtiaceae with only the more highly evolved or "average" condition of other families could create a picture of the Flacourtiaceae as being a large isolated family. I have deliberately attempted to find genera and tribes which most resemble the Flacourtiaceae, thus pointing out possible phyletic bridges. This is a long way from demonstrating phylogeny, and I would hope that these suggestions might stimulate further investigation.

Comments on miscellaneous groups occasionally placed near the Flacourtiaceae.—The Canellaceae, at one time placed in the Parietales have been demonstated (Wilson, 1964) to belong with the monosulcate Ranales closest to the Myristicaceae.

The Hoplestigmataceae have 6–9-angular, tricolporate, finely reticulate grains with a compound aperture not found in the above orders.

The Droseraceae have very specialized 7–8 porate, spinuliferous pollen. The family has possible affinities with the Centrospermae.

Sabouraea was described by Leandri (1962) and placed by him and by Hutchinson (1967) in the Flacourtiaceae. Its pollen, studied by Rethore (1963), is pantocolpate and altogether novel for the Flacourtiaceae. Its best home is still uncertain.

Barteria J. D. Hook., a myrmecophyte of west tropical Africa, has been treated as a member of the Flacourtiaceae (Wheeler, 1922). Pollen of *Barteria fistulosa* Masters is illustrated and described as being flacourtiaceous by Van Campo, Bronckers and Guinet (1965). Its pollen is spiny, polyporate, and has a diameter of about 165μ. It is not flacourtiaceous; it has been included with the Passifloraceae by Spirlet (1965).

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THE AMERICAN ERYCIBEAE (CONVOLVULACEAE): *MARIPA*, *DICRANOSTYLES*, AND *LYSIOSTYLES* I. SYSTEMATICS[1]

DANIEL F. AUSTIN[2]

ABSTRACT

Studies of morphology, anatomy, ecology, phenology, cytology, palynology, phytogeography, and an analysis of related genera form the basis of a major tribal re-arrangement in the Convolvulaceae, and a systematic study of the American members of the tribe Erycibeae. Detailed results of the palynological and anatomical studies will be reported later. Field studies in Peru, Venezuela, Guyana, and Brazil, along with greenhouse grown plants from Brazil and Panama have aided in the understanding of some of the biological relationships of the taxa. Specimens, including types, from 23 major North and South American, and European herbaria have been utilized in this study, which has led to the recognition of eleven new taxa: one new subgenus, two new sections, three new subsections, five new species, two new varieties, and two new combinations. Keys, descriptions, typification, synonymy, and specimen citation are included for each taxon.

The concept of the tribe Erycibeae has changed drastically since first conceived by Endlicher (1841) for the single genus *Erycibe*. Early workers considered the southeastern Asian genus *Erycibe* distinct from the Convolbulaceae, and some thought it best allied with the Boraginaceae (Choisy, 1833). Hallier (1893) was the first to place the southeastern Asian genus *Erycibe*, the American genus *Maripa*, and the Malagasy genus *Humbertia* in the tribe Erycibeae. Although Bentham (1846) had recognized earlier the alliance between *Maripa*, *Dicranostyles*, and *Lysiostyles*, Meisner (1869), Peter (1891), Hallier (1893), Ooststroom (1953) and others did not. Most taxonomic studies of the Convolvulaceae since Hallier have either followed his suggestions or have separated the genus *Humbertia* from the tribe (Pinchon, 1945, 1951).

Only in 1964 were the concepts of the Erycibeae and the related Dicranostyleae, both *sensu* Hallier, seriously questioned (Roberty, 1964). Although Roberty realized that the genera *Dicranostyles* and *Lysiostyles*, which had formerly been placed in the Dicranostyleae (Meisner, 1869; Hallier, 1893), were related to *Maripa* and *Erycibe*, the general superficiality of his study led most readers to disregard his publication.

There has been remarkably little study of these interesting genera since they were first described. There have been two partial revisions of the genus *Maripa* (Gleason, 1929; Falcão, 1947), but neither was very thorough. Macbride (1959)

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[1] Based on a dissertation submitted to the Graduate School of Washington University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Assisted by National Science Foundation Grant GB-5042, Air Force Office of Scientific Research Contract F44620-67-C-0055 (Walter H. Lewis principal investigator of both), the Governor Alacid Nunes Fellowship awarded by the Partners of the Alliance Pará/Missouri, a Grant-in-Aid of Research from the Society of the Sigma Xi, and field trip funds supplied by the Museu Goeldi in Belém, Brazil. Numerous people assisted in various ways and their help is gratefully acknowledged. Curators of the herbaria kindly permitted loans of their specimens for this study, and their help is acknowledged. Publication partially supported by a grant from the Division of Sponsored Research, Florida Atlantic University.

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later said for the genus that "the species as proposed seem to be very tenuous from herbarium material; a revision is much in order."

There has never been a study which included all the species of *Dicranostyles*, and most publications concerning this genus have been devoted to descriptions of new species. Barroso (1945, 1947) and Ducke (1947, 1950) debated the validity of the genus *Kuhlmanniella* which Barroso had segregated from *Dicranostyles*, but neither individual carefully examined all the species.

Morphology

1. *Maripa*

Habit: All species known are perennial, woody lianas. There have been reports of some species (*M. elongata*, *M. erecta* [= *M. scandens*], *M. glabra*, *M. panamensis*, *M. reticulata*) as trees, but these seem doubtful.

All mature specimens that I have seen in the forest have been lianas reaching the canopy. Those plants seen in Brazil climbed to the crowns of trees 30–35 m in height. Plants growing along water courses do not always reach such heights due to lack of support and may trail and twine along the margins. The *M. peruviana* seen near Iquitos, Peru, trailed for several meters along a stream, scrambling over other vegetation.

The botanical garden in Rio de Janeiro, Brazil, has living plants of *Maripa paniculata* and *M. violacea*. These plants have different habits due primarily to their method of cultivation. The former species has been trimmed and forced into an upright habit apart from any support. The two plants trained in this manner were similar in form to the cultivated liana *Wisteria* (Leguminoseae) when similarly trained. The stems were about 4–5 cm in diameter, and the plants slightly over 2 m tall.

The second species in Rio de Janeiro, *Maripa violacea*, had been provided with a large trellis. This plant covered the trellis for an area about 3 by 24 m with thick growth in all parts. The stem of the plant is about 20–25 cm in diameter and, according to Porto (1936), has been in cultivation since before 1930.

There is some variation in the mature stem size of different species. *Maripa scandens* and *M. reticulata* reach about 20–30 cm in diameter, while the largest known stem for *M. glabra* is about 15 cm—a plant collected by me near Belém, Brazil. The large majority of specimens of *M. glabra* note this species as 2–5 cm in diameter.

It has been said that all of the Convolvulaceae twine in the counter clock-wise direction (sinistrorse *sensu* De Candolle). Allard (1946) listed over thirty species of *Ipomoea*, *Convolvulus*, *Merremia*, and *Argyreia* from various parts of the world which he found to twine in this direction. All those plants which I have seen in cultivation and wild in the United States confirm Allard's statements. As a check to see if geographical location might have an effect on twining direction, O'Donell's reports of the Convolvulaceae from Argentina, Chile, and Uruguay were consulted (O'Donell, 1957, 1959*a*, 1959*b*, 1959*c*). All species illustrated in these publications were found to twine in the counter clock-wise direction.

The herbarium specimens of *Maripa*, and the living plants observed in South America, conform with the observations made by Allard, as do the seedlings

brought from south of the equator (Belém, Brazil) which are now being cultivated at the Missouri Botanical Garden and Fairchild Tropical Garden, Miami, Florida.

In the original publication of *Maripa scandens*, Aublet described and illustrated a tendril. Hallier (1893) explained this structure as the

> transformation of the leaves and assumption of other functions are up to now only known for the genus *Maripa*. In the previously mentioned specimen [*Perrottet* 292 in herb. Delessert] of *M. cayennensis* Meisn., one finds, as already pictured by Aublet in *M. scandens*, a tendril-shaped leaf reminiscent of the sprout tendril of *Strychnos*. This tendril has taken the place of the under-developed main sprout and slings itself many times like a whip strap around its stem, snail-like backwards around its axis. A similar tendril is found also in the specimens of *M. densiflora* Benth. and *M. scandens* of Poiteau in the Delessert herbarium, only here they are not connected with the mother sprout. The usual interpretation of Aublet's genus *Maripa* therefore gains new support. [Hallier, 1893: 457–458; translation by J. Boehmer and Carla Lange, 1970.]

Clearly Hallier thought that the tendrils occurring in *Maripa* were modified leaves. Anatomical studies I have made of these tendrils show that they are actually modified lateral branches.

Tendrils are known only from *Maripa scandens*, *M. densiflora*, and *M. elongata*; these organs are absent from the remaining members of the family. They are not common in those species where they do occur.

ROOTS: Very little is known about root systems in the genus, and, partially due to their size, little has been done to investigate or report them. It seems clear that plants reaching the size achieved in *Maripa* must have large, well developed roots.

It was possible to observe the upper roots of several plants of *Maripa glabra* in Belém, Brazil. The plants observed were growing in an old secondary forest ("capoeirão"), and some of the vines had been pulled from the canopy by falling trees. One of these plants had been well established on a young tree, which had fallen, carrying the vine down with it. Adventitious roots were produced at the point touching the ground where the plant had begun climbing another sapling. Although adventitious roots are not common in the Convolvulaceae, they do occur in *Dichondra*, *Ipomoea pes-caprae*, *I. aquatica*, *Iseia luxurians*, *Jacquemontia* spp., and one other *Maripa* (*M. repens*).

The young roots of the seedlings of *Maripa reticulata* brought from Brazil will be discussed under the description of seedlings.

LEAVES: The leaves are alternate or occasionally subopposite, simple, exstipulate and petiolate. The petiole is canaliculate and usually considerable wrinkled near the canal. The blade is (4–)8–20(–30) cm long and varies in shape from oblong, ovate, elliptic, obovate, or less commonly lanceolate. The base may be subcordate, obtuse, or acute; the apex obtuse, acute, shortly acuminate, or emarginate; and the margins entire.

The blades of the leaves when dried may be light to dark green, light brown, yellow-green, to grayish. Living leaves of all species are a rich green. The leaf texture varies from chartaceous to subcoriaceous and coriaceous, with most species being coriaceous. The indumentum is quite sparse on mature leaves, but closer examination will reveal scattered dibrachiate trichomes in most specimens. All species have glandular trichomes on the lower surface, and some species have stellate indument. Young leaves are commonly quite pubescent but glabrescent.

The venation is pinnate and brochidodromus, *i.e.* the secondary veins run outward but curve markedly before reaching the margin and unite with the vein above. The secondary veins are commonly impressed above and prominent below. The tertiary veins are usually reticulate, but the manner in which the reticulation is formed may be used to distinguish species groups. This will be discussed in detail in a later paper.

INFLORESCENCES: The inflorescences in *Maripa* are of dichasial character. The dichasia may be clustered together in compound-panicles (thyrses) or modified into a scorpioid cymose inflorescence. There is a strong correlation between the subgeneric groups and inflorescence type, although each group does not have exclusively one inflorescence type. Three inflorescence types are recognized: *phyllothyrsiform*, *aphyllothyrsiform*, and *racemose*.

All inflorescences originate as a lateral, axillary branch. In the phyllothyrsiform type the lateral branch is elongate, terminated by a branched dichasial flower system, and has numerous leaves at the base and among the lower flowering peduncles (Fig. 12A). The aphyllothyrsiform inflorescence is quite similar, being a lateral, axillary branch terminated by a branched dichasial flower system. It differ by the absence of leaves among the lower part of the flowering peduncles and the lower portion of the branch (Fig. 12B). This inflorescence is often much shorter than the phyllothyrsiform type, and it may be very reduced, being fasciculate, sub-racemose, or sub-umbelliform.

The third inflorescence type is highly reduced and for practical purposes may be called racemose (Fig. 12E). It is probably as in *Claytonia*, a scorpioid cyme. This inflorescence is restricted to some of the species in the subgenus *Ripama*.

The bracts are foliaceous in the lower part of the inflorescence and may be very similar to the ordinary leaves except for size. Higher on the inflorescence the bracts gradually reduce in size and may be ovate to lanceolate or occasionally triangular in shape. I have essentially followed Troll (1964) in calling every leaflike part subtending a cyme or a flower a bract.

The bracteoles are usually squamiform and triangular. They may be either persistent or caducous in the flowering stage. They are always paired, opposite or subopposite, and inserted about as far below the calyx as the calyx length.

The inflorescence of *Maripa* is clad in indument of some type in all species. The indument may be either abundant or sparse, dibrachiate, stellate, or glandular.

FLOWERS: *Calyx*—The calyx consists of five equal or slightly unequal sepals, which are free or only slightly fused at the base. Aestivation is quincuncial. In the majority of species the outer two sepals are ovate, and the inner three are

either ovate or broadly ovate, but oblong to oblong-ovate sepals occur in a few species. Pubescence in all species corresponds with that found on the other parts of the inflorescence, and, in general, with the indument on stems and leaves. The calyx is persistent in fruit and not or very slightly enlarging. The sepals may either be tightly appressed, loosely appressed, or reflexed in fruit.

Corolla—The 5-merous corolla assumes two basic forms: campanulate or funnelform. The former type usually is dissected into medium or deep lobes, and is confined to the subgenus *Ripama*. The latter type may be further subdivided into cylindric-funnelform, campanulate-funnelform, and the typical funnelform.

The outside of the corolla is pubescent with dibrachiate indument. In most species these hairs are of the unbalanced type with one branch much smaller than the other. The shortest branch may be reduced to only a knob. The indument is confined to the midpetaline areas, the interplicae. These areas of dense pubescence are corolla parts which remain exposed while the flower is in bud. The parts which were folded in bud, the plicae, are glabrous. This indument pattern reflects the plicate aestivation of the buds and may be used to distinguish *Maripa* from the related genera *Dicranostyles* and *Lysiostyles*.

Two flower colors are common in *Maripa*, white and purple. The intensity of the colors varies considerably between plants, and either color may occur in different plants of most species. Corollas are often described as pinkish.

Stamens—The five epipetalous stamens are alternate with the corolla lobes and have shaggy glandular trichomes at their triangular-dilate bases. The filaments are inserted 4–7 mm above the corolla base; they are equal in length and subulate. They reach to the sinuses of the corolla in subg. *Ripama*, but they are only about two-thirds as long as the sympetalous portion of the corolla in subg. *Maripa*. There is a disc between the bases of the filaments and the gynoecium in all species. This disc is lobed into five nectaries in all species except those of sect. *Maripa*; in sect. *Maripa* the disc is cupuliform.

The anthers are oblong to ovoid, bilocular, dorsi-fixed, latrorse or introrse, and longitudinally dehiscent.

Gynoecium—The ovary is superior, globose, conic, or cylindric, entire, and usually glabrous, although the apex is pubescent in some species. The ovary consists of two carpels and is incompletely bilocular with a partial septum in the lower portion. Each locule contains two sessile, erect, anatropous ovules attached near the inner angle; placentation is sub-basal.

The style is usually simple, although there are occasionally flowers in *Maripa reticulata* in which the style is divided almost to the base. Most species have two very short branches concealed by the enveloping stigma. There are two undivided vascular traces in the style, one terminating in each stigma lobe. The style is glabrous in all species except *M. scandens* and *M. paniculata*, where it is pubescent at the apex.

The stigmas are capitate, two-lobed, globose, cylindric, obpyriform or pyriform. They are often five to ten sulcate, apparently due to the anthers being pressed against them while in bud. The lobes are either equal or unequal with

one being larger and/or longer than the other. They may either be completely separate or somewhat fused along the apical portion.

Fruits: The fruits of *Maripa* are ligneous, indehiscent, and nut-like. They vary from ellipsoid to globose, depending on the number of seeds developing. Fruits of sect. *Maripa* are usually ellipsoid while those of sect. *Mouroucoa* are more commonly subglobose to globose. The calyx is persistent and may either be appressed against the base of the fruit or reflexed. The degree to which the calyx is appressed or reflexed is useful in determining species. The ligneous pericarp may be smooth, reticulate or striate, glossy or dull and encloses a layer of perisperm which surrounds the seed(s). The fruit is unilocular when mature, and the seed(s) push the partial septum aside.

Seeds: The number of seeds vary from one to four, because of partial abortion. The seeds are 10–22 mm long, and vary in shape depending on the number per fruit reaching maturity. If one seed develops, it is ellipsoidal; if two develop, they are flat on the inner surfaces where they touch and convex on the outer surfaces. When more than two seeds develop they are trigonous. Regardless of the number, the seeds are commonly flattened.

The testa of the seed is chartaceous or coriaceous, glabrous, and smooth; the dried perisperm often imitates a reticulate surface on the seed. In mature seeds the cartilaginous endosperm remains in only scanty traces around the embryo except in *Maripa violacea*. In this species considerable endosperm remains around the embryo.

The embryos of the Convolvulaceae are usually described as "folded" (Bentham & Hooker, 1873; Wettstein, 1944; Lawrence, 1951; Melchior, 1964) or "crumpled" (Hutchinson, 1959). Bentham and Hooker (1873) added that the embryos are often "plicatus et replicatus." While these terms are correct, they do not completely describe the folding conditions in the family. The term "contortoplicatus" has been suggested for the similar embryos of the Malvaceae, Convolvulaceae, etc. (Duke, 1969; personal communication, 1970), but this term also inadequately describes the embryos of the Convolvulaceae.

An examination of embryos in several genera of the family shows that there are two basic directions in which the embryo may be folded, and these directions are constant within genera. To establish terms for the different types of folds, the axes of the seed and embryo must be defined. The embryo is always oriented so that its base (the lower tip of the radicle) is directed toward the hylum. Therefore, the two axes are defined as follows:

Longitudinal axis—the axis lying along a line drawn connecting the hylum and the seed apex (Fig. 1A).

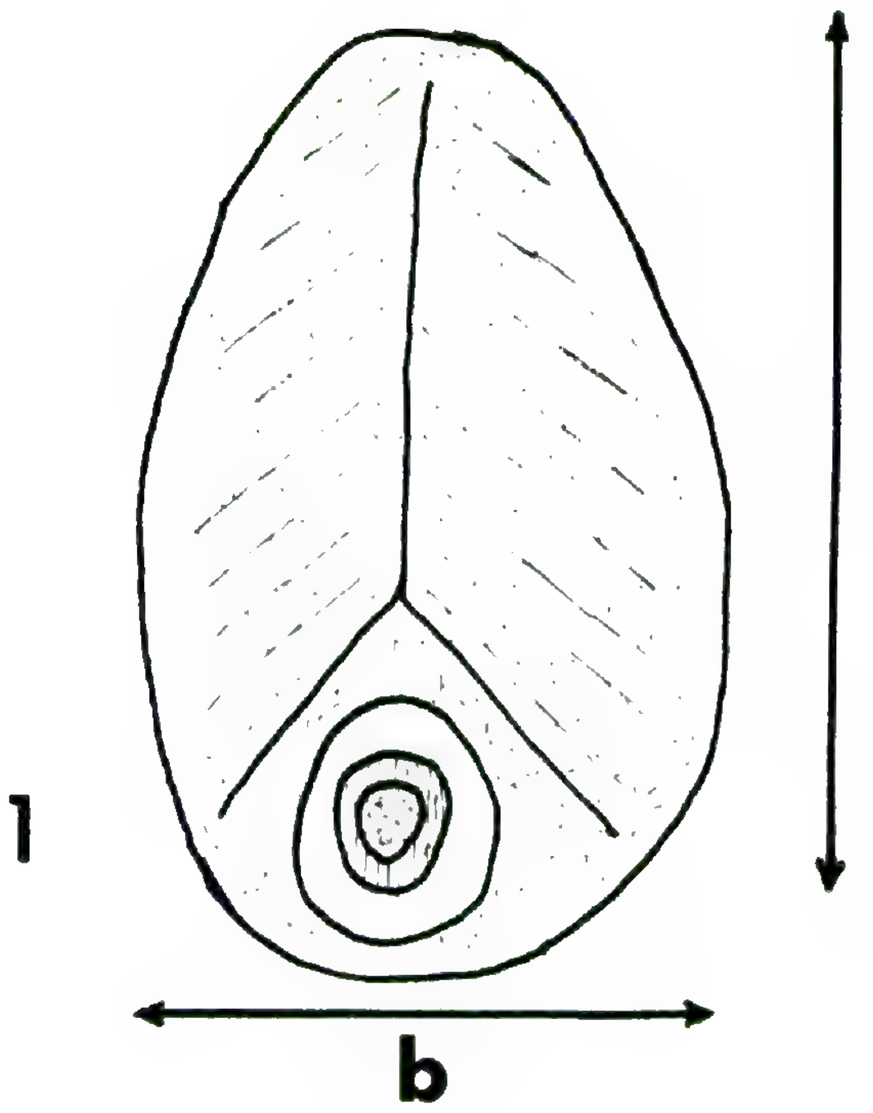
Latitudinal axis—the axis lying at right angles to a line drawn connecting the hylum and the apex (Fig. 1B).

From these definitions of the two seed and embryo axes, the two directions of cotyledonar folding may be defined:

Longiplicate—the majority of folds in the longitudinal axis (Fig. 2).

Latiplicate—the majority of folds in the latitudinal axis (Fig. 5–6).

The embryo is usually but not always folded most in one axis. The cotyledons of all species of *Maripa* except *M. violacea* are unfolded in the longitudinal axis,



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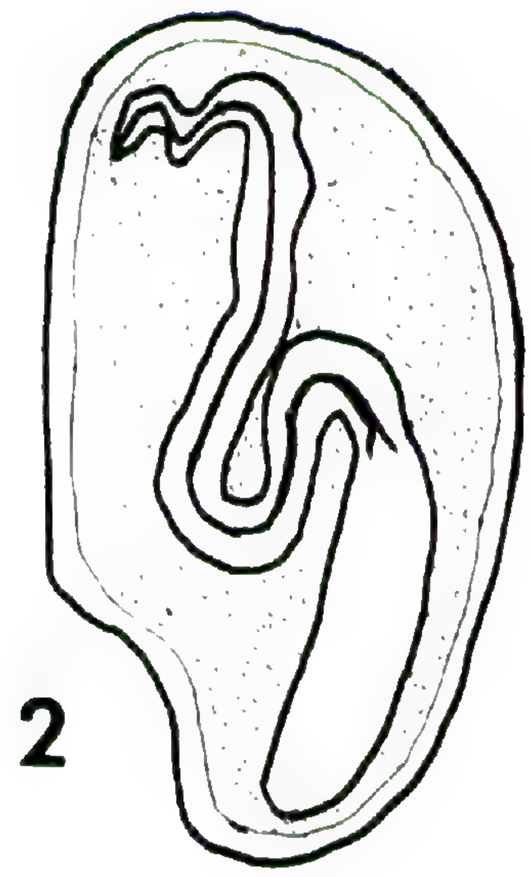

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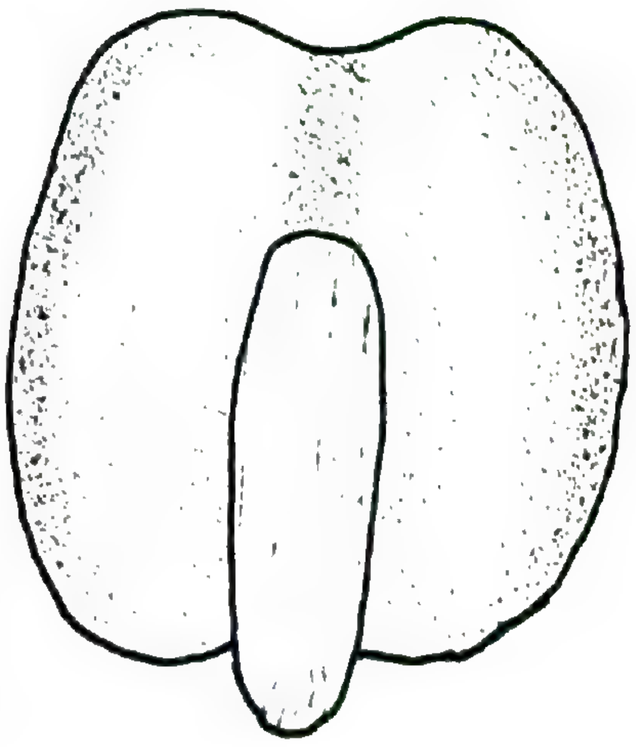

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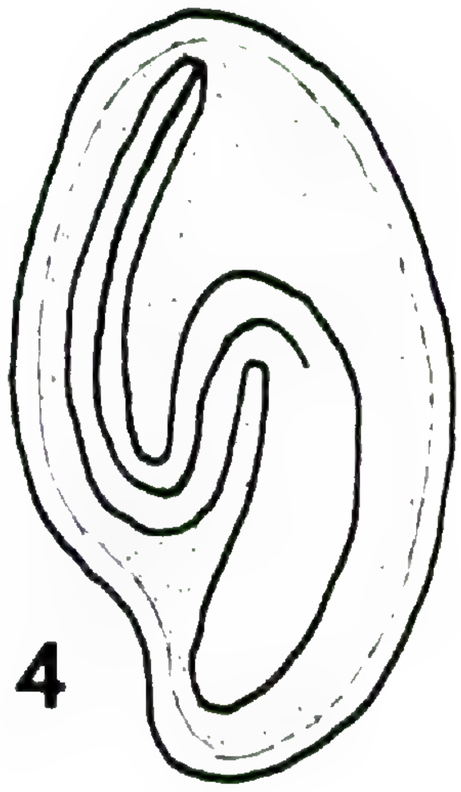

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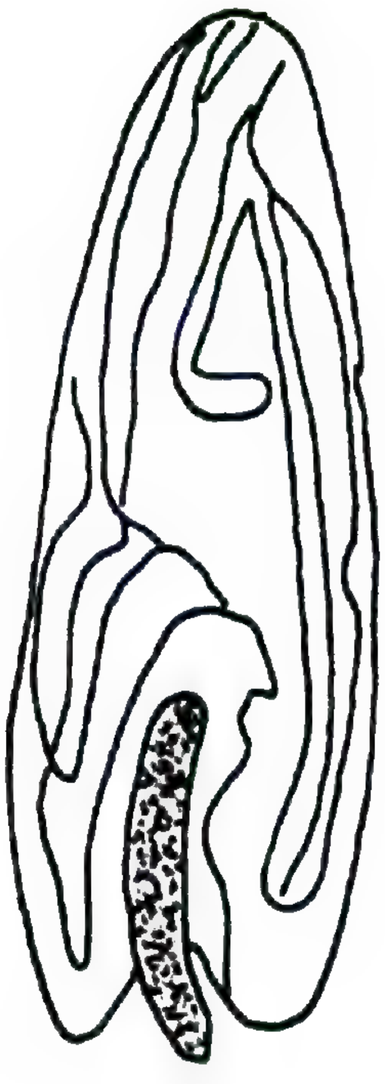

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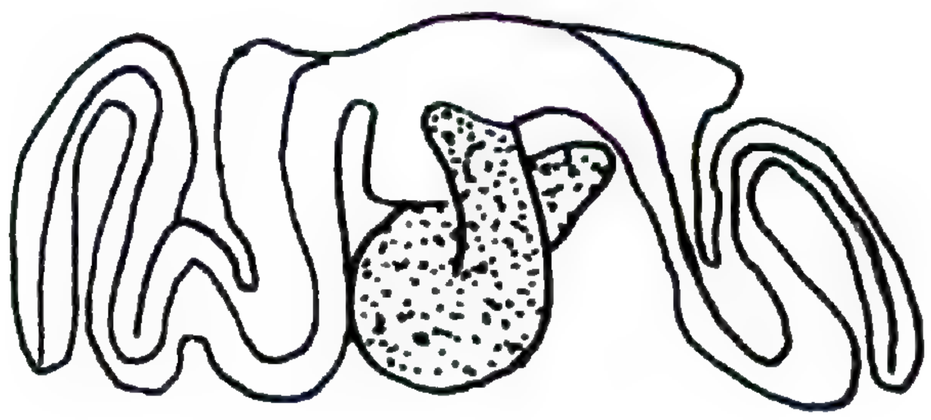


6

but folded into a V- or W-shape in the latitudinal axis; the embryos are latiplicate. In *M. violacea*, however, the amount of folding in each direction is about equal, and that species may be said to be lati-longiplicate. The cotyledons are sessile, thin in *M. violacea*, and thick in all other species. The base of the cotyledons is investing around the radicle in all species, and the apex may be rounded to emarginate. The radicle is short and almost completely invested in all species except *M. violacea*, in which it is about as long as the cotyledons and free from them.

SEEDLINGS: Only seedlings of *Maripa reticulata* have been studied. The following account of seed germination and seedling growth is largely based on observations made during the summer of 1969 at the Agronomical Institute (Instituto de Pesquisas e Experimentação Agropecuarias do Norte) in Belém, Brazil.

From a vine growing about 35 m up on a rubber tree (*Hevaea brasiliensis* M. Arg.), numerous seeds had fallen onto "várzea" soil. Most of the seeds had been removed from the ligneous exocarp (perhaps by monkeys), while a few were still contained within it. The seeds still enclosed in the exocarp were fracturing the fruit by swelling, and in all cases observed, the cotyledons left the exocarp first, reversing the usual procedure where the radicle exits first. The radicle usually was curled around the inside of the partially broken fruit coat. Seeds in this condition were not seen becoming established, while seeds which had been freed of the exocarp were becoming established readily.

The sequence of events in germination and the first stages of establishment seem to be:

1.) The radicle penetrates the chartaceous testa, which still surrounds the seeds in all cases, and starts growing toward the substratum. Germination need not take place on the soil itself, and several seeds were found in the first stages on the leaf cover of the forest floor.

2.) When the radicle has reached the substratum and penetrated far enough to give some support and absorption, the epicotyl begins to grow. During the first stages of epicotyl growth the developing plant becomes oriented in an upright position.

3.) After the proper period of growth, the epicotyl becomes large enough to force the cotyledons apart; the testa often clings to the apex of one of the cotyledons. During the period within the seed the cotyledons are fairly thick, but as soon as they are freed of the testa they become thinner and more foliaceous. They remain longitudinally folded, however, until they are shed. The sessile cotyledons are glabrous, but they may have scattered oil glands.

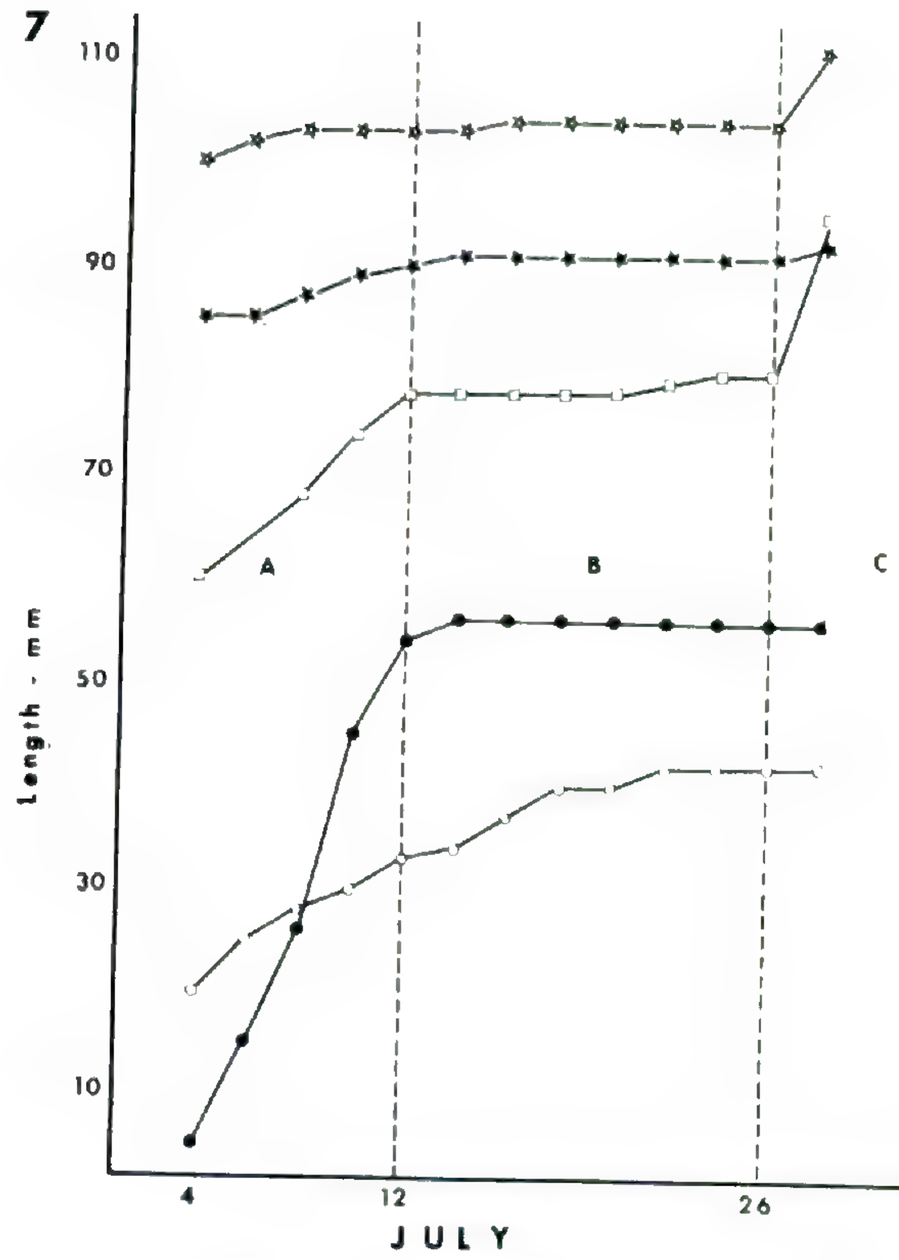
←

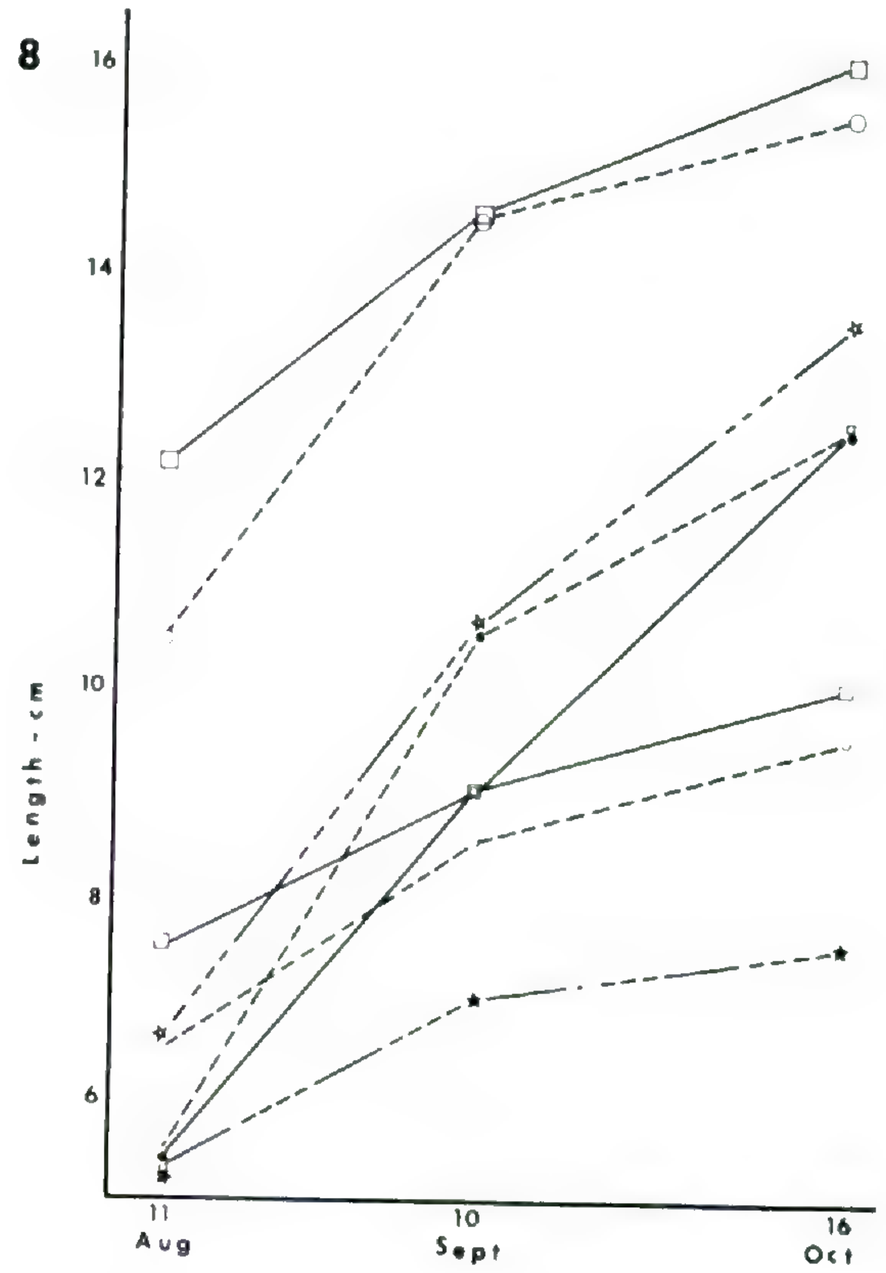
FIGURES 1–6. Embryos of the Convolvulaceae.—1. Convolvulaceous seed (diagrammatic). a. Longitudinal axis. b. Latitudinal axis.—2. *Calystegia sepium* (redrawn from Baillon, 1891); longitudinal section showing longiplicate embryo.—3. *Maripa* (*Mouroucoa*) *violacea*; longi-latiplicate embryo in face view, note lateral folds.—4. *M. violacea*; longitudinal section.—5. *Bonamia* (*Trichantha*) *trichantha*; latiplicate embryo, radicle stippled.—6. *B. trichantha*; cross-section made just above radicle, lateral folds on each side of the stippled radicle.

TABLE 1. Growth of *Maripa reticulata* seedlings during first month after germination. Seedings collected on the IPEAN grounds at the Várzea do Aurá (A.P.E.G.); quadrant 366-93, on 3 July 1969.

Date July	Plant number				
	1	2	3	4	5
4	5 mm	20 mm	60 mm	85 mm	100 mm
6	15	25	—	85	102
8	26	28	68	87	103
10	45	30	74	89	103
12	54	33	78	90	103
14	56	34	78	91	103
16	56	37	78	91	104
18	56	40	78	91	104
20	56	40	78	91	104
22	56	42	79	91	104
24	56	42	80	91	104
26	56	42	80	91	104
28	56	42	95	92	111

4.) As the epicotyl grows, the eophylls (the first two true leaves) expand and enlarge. When the young stem has grown about 10–15 days, apical growth almost stops (Table 1), and the eophylls expand to their maximum size. This expansion is completed after about 25–30 days, and apical growth is resumed. This sequence of events is graphically illustrated in Fig. 7–8.





FIGURES 7–8. Seedling growth rates of *Maripa reticulata*.—7. During first month after germination. A. Apical growth. B. Eophyll expansion. C. Apical growth.—8. During second, third, and fourth months after germination. Data from Table 2. Square = sun grown; circle = shade grown; star = mist grown.

TABLE 2. Growth of *Maripa reticulata* seedlings during second, third, and fourth months after germination.

	Date			Total size increase
	11 Aug.	10 Sept.	16 Oct.	
Shade				
1.	7.0 cm	10.0 cm	11.0 cm	4.0 cm
2.	5.5	10.5	12.5	7.0
3.	6.5	8.5	9.5	3.0
4.	—	—	—	—
5.	13.5	15.2	15.5 (2 stems)	2.0
6.	10.5	14.5	15.5	5.0
7.	7.0	11.5	12.5	5.5
8.	7.3	9.5	11.0	3.7
Sun				
9.	7.5 cm	9.0 cm	10.0 cm	2.5 cm
10.	5.4	9.0	12.5	7.1
11.	7.5	9.5	10.5	3.0
12.	11.2	14.5	19.0	7.8
13.	12.2	14.5	16.0	3.8
Mist				
14.	6.0 cm	10.0 cm	— cm	— cm
15.	6.0	9.0	9.5	3.5
16.	5.4	7.0	7.5	2.1
17.	6.7	8.5	9.5	2.8
18.	6.5	10.5	13.5	7.0
19.	7.2	9.5	10.5	3.3

5.) The seedlings were collected on 3 July 1969, and by October 1969 most plants had produced two leaves in addition to the first two eophylls. By January 1970 the plants averaged three leaves beyond the two eophylls.

It is clear that the growth rates beyond the decimeter stage were slower than normal. These were undoubtedly slowed by the shock of being moved from Brazil to the United States. Growth was further slowed by confinement of the roots. Each time the plants were re-potted there was a period of rapid growth while the roots filled the empty soil. As soon as the roots occupied the soil, growth almost stopped.

The most adverse affects noted by being transferred from Brazil to the United States were a shedding of the eophylls and absortion of the apical meristem. This apical abortion occurred in many of the plants which had shed their eophylls. In every case of eophyll loss and/or apical meristem abortion, the stem resumed growth. Many of the plants in which the apical meristem died produced a second stem along with the original. A mechanism similar to this may have produced the plants reported as having "fasciculated stems" (*M. nicaraguensis, Austin-Smith H1616*).

The seedlings were separated into three groups and grown in full shade, full sunlight, and in a shaded mist chamber (Table 2). Plants growing in the sun lost their cotyledons first, those in the shade second, and those in the mist last.

One plant in the mist for three months still retained one cotyledon, while all other plants had shed them. By the second month most plants had lost their cotyledons.

Lateral branches on the primary root begin to grow at about the same time as the epicotyl. By the time the epicotyl is about one centimeter long there may be as many as five lateral branches on the primary root. The first lateral may be produced near the cotyledons, or nearer the primary root tip. The root system observed in the seedlings of *Maripa reticulata* was monopodial with lateral branches extending into the soil at right angles to the main root axis.

2. *Dicranostyles*

HABIT: While several species have been reported as trees and shrubs, most reports describe the plants as perennial, woody lianas. The living plants I have seen were all lianas.

Mature individuals in the forest climb 30–35 m to the top of the canopy where the foliage is produced. Height varies considerably and depends on the character of the supporting arborescent vegetation.

Stems of the plants I saw in Brazil were smaller than the stems of *Maripa*, and this size difference is substantiated by data from herbarium specimens. The direction of twining conforms with *Maripa*.

ROOTS: Undescribed and not seen.

LEAVES: The leaves are alternate, simple, exstipulate and petiolate. Petioles are canaliculate and normally wrinkled near the canal. The blade is ca. 4–40 cm long and oblong, elliptic, obovate or lanceolate. The base may be cordate, obtuse or acute; the apex obtuse, acute, acuminate, or emarginate; and the margins entire. The blades when dried vary from green to dark brown. Living leaves are rich green or colored by the indument. Leaf texture varies from subcoriaceous to membranaceous, with most species being chartaceous. Indumentum varies from glabrescent to quite dense in different species. Trichomes are small and mostly dibrachiate, usually appressed. There are erect trichomes on the lower leaf surface of *Dicranostyles laxa* and *D. globostigma*.

Venation is pinnate and brochidodromus. The secondary veins are commonly impressed above and prominent below. The tertiary veins are reticulate, the areoles being mostly closed with some unbranched or slightly branched veins included. The branching pattern of the veins is almost identical with *Lysiostyles* and *Maripa* subg. *Ripama* and will be described in detail in a later paper.

INFLORESCENCES: The inflorescences in *Dicranostyles* are dichasial with dichasia clustered into compound-panicles or modified into scorpioid cymose groups. Most species are aphyllothyrsiform, but there are some with racemose inflorescences (for terms see discussion of inflorescences of *Maripa*). The inflorescence of *D. densa* is highly modified and reduced to a dense cymose cluster. The only species which approaches the phyllothyrsiform condition is *D. falconiana* where some reduced leaves may occur near the base of the main axis.

The bracts are squamiform and usually ovate to triangular or deltoid-triangular; the bracteoles are also squamiform and usually triangular. They may

be either persistent or caducous, with the bracteoles paired and opposite or subopposite.

Indument of some type covers the inflorescences of most species. The indument is usually dense, appressed, and dibrachiate.

FLOWERS: *Calyx*—The calyx is composed of five equal sepals, which are free or only slightly fused at their bases. Aestivation is quincuncial. Sepal shape varies, but the outer two sepals are usually deltoid-ovate and the inner three either ovate or broadly ovate. Pubescence, when present, conforms with that found on other parts of the inflorescence, although it may be confined to the exposed portions of the sepals. The calyx persists in fruit and is very slightly enlarging. Sepals are reflexed in the fruits of all species where fruits are known.

Corolla—The pentamerous corolla may be subrotate, campanulate or funnelform. The former two types are dissected into lobes which are mostly longer than the sympetalous tube and are characteristic of the subg. *Dicranostyles*. The latter type is confined to the subg. *Kuhlmanniella* where the lobes are mostly shorter than the sympetalous tube.

The outside of the corolla is pubescent with dibrachiate indument. This indument is found on all parts of the corolla lobes, reflecting the valvate aestivation of the buds.

Flowers have been described as white or pink. They are occasionally said to be "ferrugineous," but this is probably due to the indument.

Stamens—The five epipetalous stamens are alternate with the corolla lobes. The filaments may be attached near the corolla tube base or apex. If attached near the base, they may be either glabrous or glandular pubescent; while if attached at the tube apex, they are always glabrous. In the latter condition the inside of the tube may be glabrous or it may have a row (or rows) of glandular trichomes about halfway between the base and the apex. The filaments are of equal length, subulate, and excluded between the corolla lobes in all species except *Dicranostyles densa* and *D. villosus*. In these two species the filaments are introrsely recurved at the apex and included within the corolla. There is a cupuliform, five-lobed disc in most species.

Anthers are mostly oblong in subg. *Dicranostyles* and trianguloid in subg. *Kuhlmanniella*. They are versatile, bilocular, dorsifixed, latrorse or introrse, and longitudinally dehiscent.

Gynoecium—The ovary is superior, ovoid to obovoid, entire, mostly pubescent, at least at the apex. It consists of two carpels and is incompletely bilocular with a partial septum in the lower portion. Each locule contains two sessile, erect, anatropous ovules; placentation is sub-basal.

The styles are divided to the base or fused almost to the apex in subg. *Dicranostyles*. In subg. *Kuhlmanniella* the styles are entire and without branches. There is one undivided vascular trace in each stylar branch, or, if the style is entire, two traces. The styles are completely glabrous, pubescent for about the lower half, or rarely completely pubescent.

The stigmas are capitate, occasionally irregularly complanate, two lobed or two completely free, cylindric, or obpyriform. The lobes are usually equal in size, but one may be placed slightly higher than the other when cylindric or

obpyriform. They may be either completely separate and readily visible (subg. *Dicranostyles*) or closely appressed and not easily distinguishable (subg. *Kuhlmanniella*).

FRUITS: Fruits of *Dicranostyles* are similar to those found in *Maripa* and are ligneous, indehiscent, and nut-like. The number of seeds reaching maturity does not appear to have as great an effect on fruit shape, as it does in *Maripa*, since the fruits are mostly ellipsoid. Obpyriform fruits occur in *D. ampla* var. *attenuata*. The calyx is persistent and reflexed from the fruit base to about 180°. The ligneous pericarp may be smooth, reticulate, rugose, and/or striate, glossy or dull and encloses a layer of perisperm which surrounds the seed(s). The fruit is unilocular when mature, and the seed(s) push the partial septum aside as in the other members of the tribe.

SEEDS: The number of seeds varies from one to four due to partial abortion. The seeds are 15–20 mm long and vary in shape depending on the number per fruit as in *Maripa*.

The testa of the seed is chartaceous or coriaceous, glabrous and smooth; the dried perisperm often imitates a reticulate surface on the seed as in *Maripa* and *Lysiostyles*. In mature seeds the cartilaginous endosperm is scanty or absent. The embryos are latiplicate in the species examined. Cotyledons are sessile, thin and foliaceous, with the base investing the radicle and the apex rounded. The radicle is less than half the length of the folded cotyledons and bent near the point of attachment.

3. *Lysiostyles*

HABIT: Plants of *Lysiostyles* are perennial, woody lianas. Mature individuals have much the same habit as *Dicranostyles* and *Maripa*.

ROOTS: Undescribed and not seen.

LEAVES: The leaves are alternate, simple, exstipulate, and petiolate. The petiole is canaliculate and wrinkled near the canal. The blade is 7.5–14 cm long and oblong to elliptic or obovate. The base is obtuse, the apex shortly acuminate, and the margins entire. The blades when dried are yellow-brown; leaf texture is coriaceous. The indument is dense and reddish on the lower surface of the leaves, while the upper surface is glabrescent. The trichomes are T-shaped, small, and appressed.

The venation is pinnate and brochidodromus with the secondary veins deeply impressed above and prominent below. The tertiary veins are reticulate, the areoles being mostly closed but with some unbranched or slightly branched veins included. The branching pattern is similar to *Dicranostyles* and *Maripa* subg. *Ripama*. This will be described in detail in a later paper.

INFLORESCENCES: Inflorescences of *Lysiostyles* are aphyllothyrsiform.

The bracts are squamiform and triangular; the bracteoles are also squamiform and triangular. They are persistent, and the bracteoles are paired and opposite or subopposite.

The indument of the inflorescence is dense, appressed, and dibrachiate.

FLOWERS: *Calyx*—As in *Dicranostyles*.

Corolla—The pentamerous corolla is subrotate. The lobes are pubescent

outside with dibrachiate indument, which is found on all parts, reflecting the valvate aestivation of the buds. Color has been described as white.

Stamens—The five epipetalous stamens are alternate with the corolla lobes. The filaments are attached near the base of the corolla tube and are glandular pubescent at the dilate-triangular base. The dilate portion of the filament base is laterally elongate and fused, producing a ring of filament-derived tissue around the inside of the corolla tube. The filaments are of equal length, subulate, and excluded between the corolla lobes. There appears to be no disc.

The longitudinally dehiscent thecae are oblong and attached near the base of a broad, elongate connective which extends considerably past their apex. The long, flattened connective is normally folded in such a manner that the thecae are effectively extrorse.

Gynoecium—The ovary is superior, globose, entire, and pubescent on most of the upper portion. It consists of two carpels and is incompletely bilocular as in *Maripa* and *Dicranostyles*. Each locule contains two erect, anatropous ovules, placentation is sub-basal.

The glabrous styles are shortly branched to divided to the base. The amount of separation of the two stylar branches appears to be related to maturity, *i. e.* the older a flower, the more the stylar separation.

The stigmas are cylindrical, two lobed or two completely free. The lobes are more or less equal in size or with one slightly longer than the other.

Fruits: Fruits of *Lysiostyles* are similar to those of *Maripa* and *Dicranostyles*. They are ellipsoid and one-seeded. The calyx is persistent and reflexed from the fruit base to about 180°. The ligneous pericarp is slightly thicker than in the thickest species of *Dicranostyles*, deeply rugose, dull and buff-gray. The perisperm is similar to *Maripa* and *Dicranostyles*.

Seeds: The fruits examined contained only one seed, which was 16–18 mm long and ellipsoid.

The testa is coriaceous, glabrous and smooth, and the perisperm as in *Maripa* and *Dicranostyles*. Endosperm is scanty or absent, and the embryos are latiplicate. Cotyledons are sessile, thin and foliaceous, with the base investing the radicle, and the apex rounded. The radicle is less than half the length of the folded cotyledons and bent near the point of attachment.

Seedlings: Undescribed and not seen.

Pollination

Flower visitors for only three species have been reported. Porsch (1929: 223) lists hummingbirds as visitors for *Maripa violacea*. Flowers of this plant are blue and do not conform to the floral features normally associated with the hummingbird syndrome of pollination described by Grant and Grant (1968) and others. It is feasible, however, that some successful pollination might be accomplished by the birds due to the position of floral parts; it is unlikely, however, that they play the major role in pollination of the species. *Maripa reticulata* and *Dicranostyles ampla* were studied by the Entomology section of IPEAN (Instituto de Pesquisas e Experimentação Agropecuarias do Norte) in Belém, Brazil. Their studies have not yet been completed, and all the data have not been compiled.

Yet, Dr. Domeciano Días, director of the entomological studies at IPEAN, has provided the following data about two plants collected at the study area on the "várzea" of the Guamá River near the Igarape Aurá on the IPEAN ecological study reserve APEG (Area de Pesquisas Ecologicas do Guamá).

Maripa reticulata—Location APEG 423–7.

Flower color: white, 10–15 mm long, campanulate. Blooming period: ending 25 January 1966. Visiting insects: Diptera, Hymenoptera (Vespidae, Apoidea), and Coleoptera (collection numbers 165–166). Comments: Mixed insects with short tongues. All are medium-sized insects. Probably all after nectar.

Dicranostyles ampla—Location APEG 183–100.

Flower color: white, 3–4 mm long, subrotate. Blooming period: middle 17 October 1967. Visiting insects: Diptera, Hymenoptera (Vespidae, Apoidea, Formicidae), and Coleoptera (some with very long tongues) (collection numbers 105–110). Comments: mixed insects, some of the Coleoptera with tongues about as long as the body. Medium- to large-sized insects. The ants (Formicidae) and wasps (Vespidae) included several predators. Most of the visitors were probably after nectar and not pollen.

The generalized data as here presented give very little impression about insect relations and pollination. Dr. Días and his colleagues are continuing the analysis of insect-plant relations in the IPEAN area and plan to publish a species list of insects and plants which will include statements about ecological relations.

It is paradoxical that the largest insects (excluding predators) and those with the longest tongues were found on the small flowers of *Dicranostyles* and not on the larger flowers of *Maripa reticulata*.

A common visitor to both species was the heterogeneous genus *Trigona* (Hymenoptera: Apoidae) (Días, personal communication). These small bees must be important in pollinating the plants. There may have been several species of this bee genus involved, but it must be significant that both these plant species have similar corollas, and both were visited by similar groups of insects.

CYTOLOGY

Only one species for the tribe Erycibeae has been examined cytologically. This species is:

Maripa reticulata Ducke. $2n = 30$. BRAZIL. PARÁ: Belém, Várzea do Aurá (A.P.E.G.) at IPEAN. Seedlings germinating below liana climbing ca. 35 m into a rubber tree (*Hevaea brasiliensis* M. Arg.), *Austin 4214* (FAU, IAN, MO).

The data in Table 3 summarize the cytological counts for the entire convolvulaceae and the related Cuscutaceae without giving specific details on each report. These data were largely taken from Darlington and Wylie (1945), Cave *et al.* (1959, 1961), and Ornduff (1967, 1968, 1969). Modern base numbers for the Convolvulaceae are 9, *10*, *11*, *12*, 13, 14, and **15**; for the Cuscutaceae $x = 7$ and 15 (common numbers are in *italic*; the most common in **boldface**). The chromosome data would suggest that an important base number in the Cuscutaceae has been 7 (Table 5), but this number has been much less important

in the derivation of the Convolvulaceae (Tables 4 and 6). Since the high base numbers must certainly be paleo-polyploids, the scheme proposed by Skovsted (1941) can perhaps be applied to the Convolvulaceae to gain insight into the paleo-base number (Table 6). These data suggest that either $x = 5$ or $x = 6$ were

TABLE 3. Chromosome numbers of the Convolvulaceae and Cuscutaceae.

CONVOLVULACEAE

1. *Aniseia* $2n = 60(2)$.[a]
2. *Argyreia* $2n = 28(1)$, $30(1)$.
3. *Bonamia* $2n = 30(1)$.
4. *Calystegia* $2n = 20(1)$, $22(2)$, $24(1)$.
5. *Calonyction* $2n = 30$.
6. *Calycobolus* $2n = 28(1)$.
7. *Convolvulus* $2n = 18(3)$, $20(5)$, $22(7)$, $24(3)$, $26(1)$, $30(4)$, $36(2)$, $40(1)$, $44(2)$, $48(1)$, $50(2)$.
8. *Cressa* $2n = 28(2)$.
9. *Dichondra* $2n = 30(1)$.
10. *Evolvulus* $2n = 24(2)$.
11. *Exogonium* $2n = 24$–$28(1)$.
12. *Hewettia* $2n = 30(13)$.
13. *Ipomoea* $2n = 28(1)$, $30(59)$, $60(1)$, $90(3)$.
14. *Jacquemontia* $2n = 18(6)$, $20(2)$.
15. *Merremia* $2n = 28(4)$, $30(3)$, $58(1)$.
16. *Neuropeltis* $2n = 28(1)$.
17. *Operculina* $2n = 30(3)$.
18. *Porana* $2n = 26(2)$.
19. *Quamoclit* $2n = 28(3)$, $30(4)$, $58(1$, $28\times$, 30 hybrid).
20. *Stictocardia* $2n = 30(1)$.
21. *Stylisma* $2n = 28(2)$.

CUSCUTACEAE

1. *Cuscuta* $2n = 14(1)$, $28(3)$, $30(3)$, $32(1)$, $42(3)$, $56(3)$, $60(2)$.

[a] Numbers in parentheses equal number of individual counts.

TABLE 4. Ploidy Levels in the Convolvulaceae.

| | | |

TABLE 6. Hypothetical base numbers in the Convolvulaceae. Numbers in parenthesis can be derived from more than one base; dotted lines connect numbers which may be derived in different manners. Solid lines connect known aneuploids.

	2×	3×	4×	5×	6×	8×	10×	12×	15×	18×
x = 5			20		(30)	(40)	(50)	(60)		(90)
x = 6		(18)	(24)	(30)	(36)	(48)	(60)		(90)	
x = 7			28							
x = 8		(24)			(40)	(48)				
x = 9	(18)		(36)				(90)			

important in the paleo-Convolvulaceae. The numbers $x = 7$ and 8 seem to have been much less important or perhaps nonexistent.

It should be clear from these scanty data that all comments concerning paleo-base numbers in the Convolvulaceae are highly theoretical. Many more counts are needed before a definite statement can be made concerning the cytology of the paleo-Convolvulaceae. It is certain, however, that the majority of modern genera examined in the Convolvulaceae are either $x = 15$ or derived from that base; about ten genera are based on 15, and several others (*e. g. Stylisma*, *Neuropeltis*, etc.) are apparently derived from this base. Along with the $x = 15$ line a second major line of evolution based on $x = 10$–12 dominates the tribe Convolvuleae. Aneuploidy and aneusomity are found within many species and individuals in the family (Sharma & Chatterji, 1957; Sharma & Datta, 1958), and, because of these phenomena, it is difficult to establish which of the bases might be the most ancient. The $x = 10$–12 line could have been derived from the $x = 15$ by descending aneuploidy, but, in view of the data available, this seems unlikely. It is more likely that the $x = 10$–12 group gave rise to that with $x = 15$.

The data available for the Erycibeae indicate that the tribe is a member of the $x = 15$ line of evolution.

EVOLUTION OF ORGANS

Evolutionary trends in several morphological characters of the American members of the Erycibeae are summarized in the following discussion. Although most trends are described in the preceding sections of the text, further clarification is given here. The species used to represent the different stages do not form a phylogenetic series.

EVOLUTIONARY TREND IN STIGMAS

The stigmas of the Erycibeae probably originated from filiform types with a restricted stigmatic surface (Fig. 9A). The ancestral types were perhaps similar to the stigmas now found in *Convolvulus* (F. Sa'ad, 1967). These filiform stigma lobes became reflexed and appressed (Fig. 9B), and eventually restricted

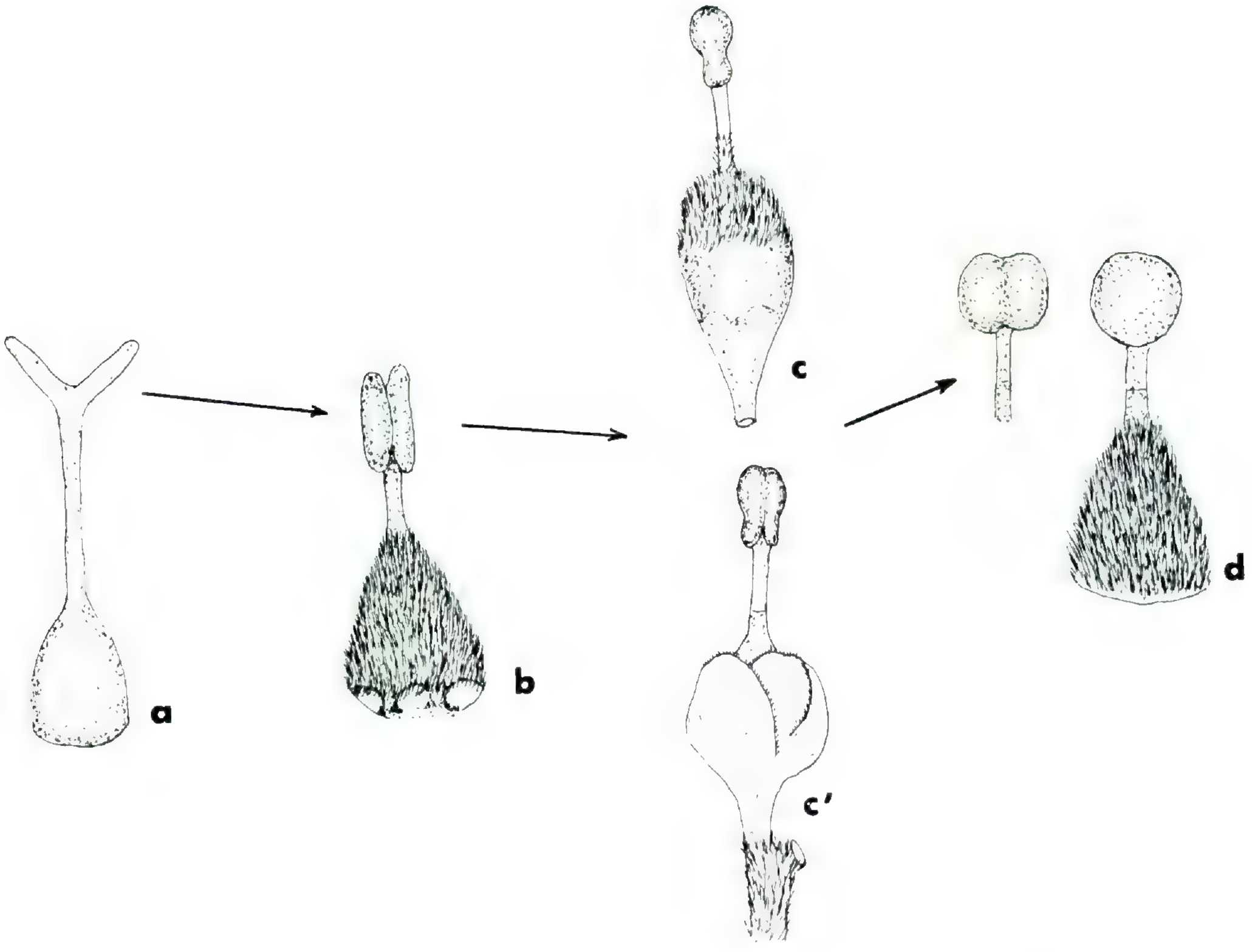


FIGURE 9. Evolutionary trend in stigmas.—A. Hypothetical prototype.—B. *Dicranostyles falconiana*.—C. *D. integra*.—C'. *D. holostyla*.—D. *D. globostigma*.

at the base (Fig. 9C, 9C'). The restriction at the base led to subglobose capitate stigmas (Fig. 9D).

The hypothetical ancestor is absent from *Dicranostyles*, but all other stages are found in that genus. Stigmas of *Lysiostyles* are similar to those of *Dicranostyles falconiana*, while in all species of *Maripa* they are globose and capitate as in *D. globostigma*.

EVOLUTIONARY TREND IN STYLES

Myint (1966) suggested that in *Stylisma* (tribe Cresseae) there has been a progressive fusion of the stylar branches. A similar trend is found in the members of the Erycibeae. The most primitive style has two stylar branches completely free to the base (Fig. 10A). From this free condition a progressive fusion of branches has occurred (Fig. 10B–C). Occasional collections of *Maripa* subg. *Ripama* will have the branches half-fused in some flowers, completely fused in others. Styles of *Lysiostyles* are also variable, ranging from completely separate (Fig. 10A) to almost fused (Fig. 10C). The species of *Maripa* subg. *Maripa* and some species of *Dicranostyles* have very short branches concealed by the stigma (Fig. 10D). Two species of *Dicranostyles* have very short styles (Fig. 10E) reminiscent of those found in *Erycibe* (Ooststroom, 1953).

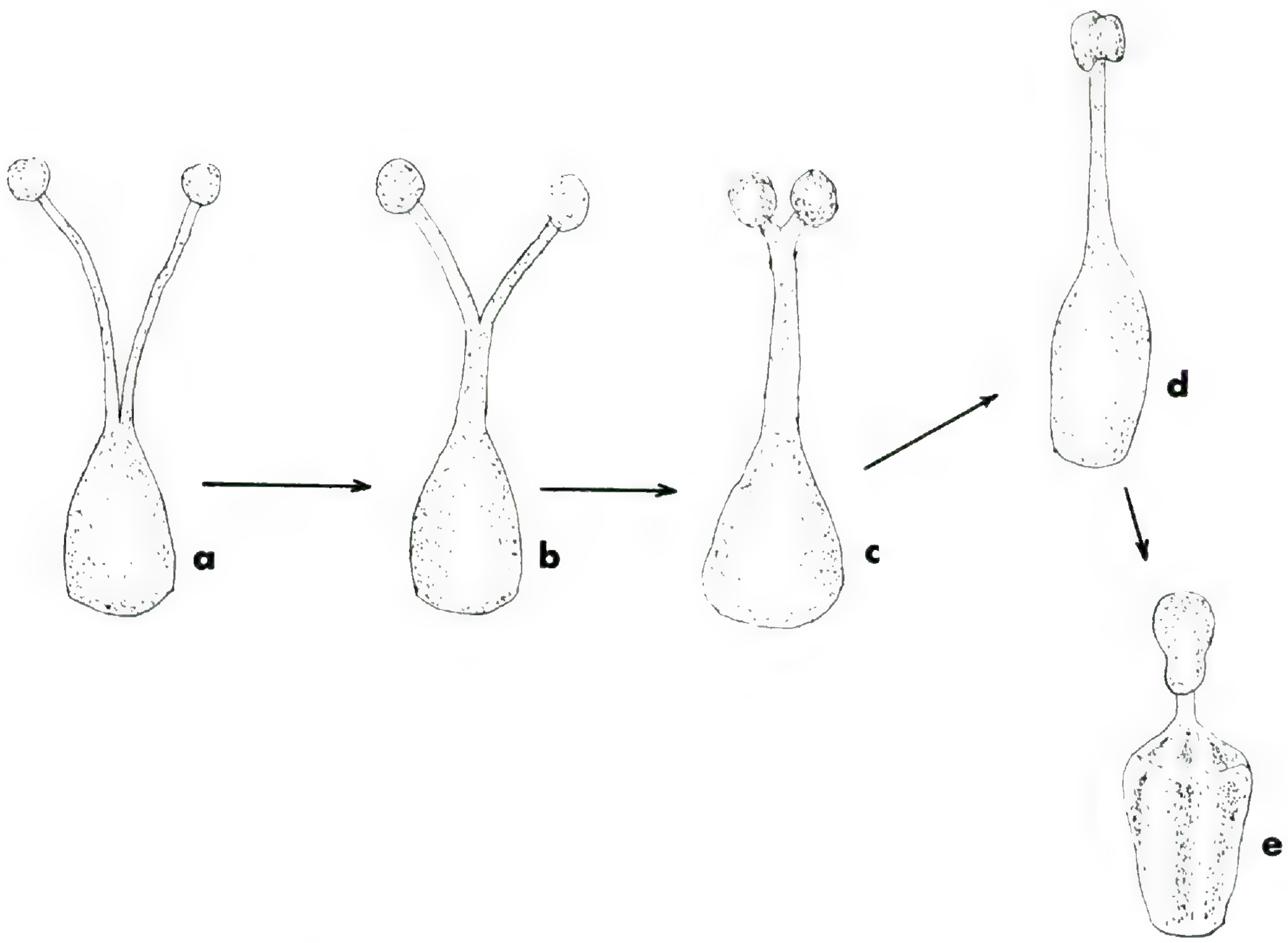


FIGURE 10. Evolutionary trend in styles.—A. *Dicranostyles ampla*.—B. *D. densa*.—C. *D. longifolia*.—D. *D. guianensis*.—E. *D. mildbraediana*.

EVOLUTIONARY TRENDS IN STAMENS

The most primitive type stamens are attached near the base of deeply lobed corollas (Fig. 11A–B), much as they are in the Polemoniaceae (Grant, 1959). As in the Polemoniaceae, a fusion of the filaments with the corolla has occurred (Fig. 11C–E). Associated with this fusion has been either a loss (Fig. 11B, D) or an enhancement (Fig. 11E) of the glandular trichomes normally found near the base of the filaments. Stamens of *Maripa* and *Lysiostyles* are attached near the corolla base and are always glandular.

EVOLUTIONARY TRENDS IN INFLORESCENCES

There appear to have been two basic directions to reduction in inflorescence complexity: reduction of the dichasium and loss (or compression) of the nodes. Both of these trends have usually resulted in simpler inflorescences. The trends have the following distinct stages.

A. *Phyllothyrsiform*: a lateral branch with normal leaves at the base which grade into bracts toward the apex: inflorescence branches mixed with leaves away from lateral branch base; apex of lateral branch without leaves, having only bracts and thyrsiform flowering system (Fig. 12A).

B. *Aphyllothyrsiform*: a lateral branch arising from a leaf axil as in A; without leaves along the length of the lateral branch (Fig. 12B).

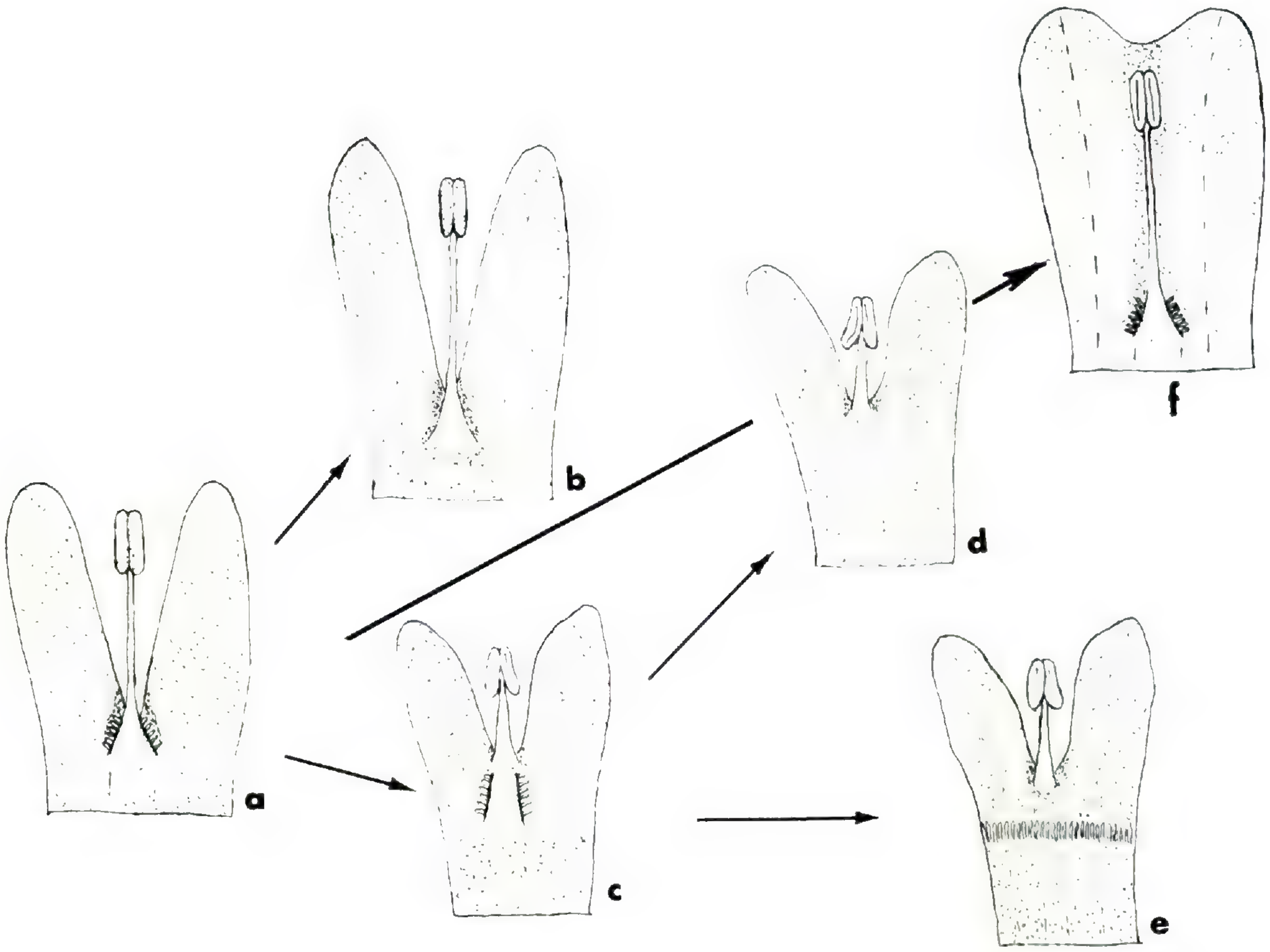


FIGURE 11. Evolutionary trends in stamens.—A. *Dicranostyles scandens*.—B. *D. longifolia*.—C. *D. sericea*.—D. *D. falconiana*.—E. *D. integra*.—F. *Maripa scandens*.

C. *Clustered Aphyllothyrsiform*: a lateral branch inflorescence as in B. The main axis from which the lateral branches are produced has apparently been reduced by loss of nodes to provide the clustering of the inflorescences (Fig. 12C).

D. *Reduced Aphyllothyrsiform*: a lateral branch inflorescence as in B, but the lateral axis much reduced and often fasciculate-branched. This form may be sub-umbelliform to sub-racemose (Fig. 12D).

E. *Racemose*: technically a scorpioid cyme; the cymes have been reduced so that only one flower remains (Fig. 12E). There is further reduction in the genus *Humbertia* where only solitary flowers occur in leaf axils.

EVOLUTIONARY TRENDS IN POLLEN

It is generally agreed that zonocolpate grains are more primitive than pantocolpate grains (S. I. Saad, 1961; Stern, 1962; Tsukada, 1964; Manitz, 1968). That the former gave rise to the latter is supported not only by modern data but also by fossil data (Kuprianova, 1969).

In the Erycibeae, as in the Cactaceae (Tsukada, 1964), small compacted bacula are considered more primitive than irregularly scattered bacula of mixed size (Fig. 13). The branched bacula of *Maripa* have apparently been derived from unbranched bacula through lateral fusion. The shift from small, compacted

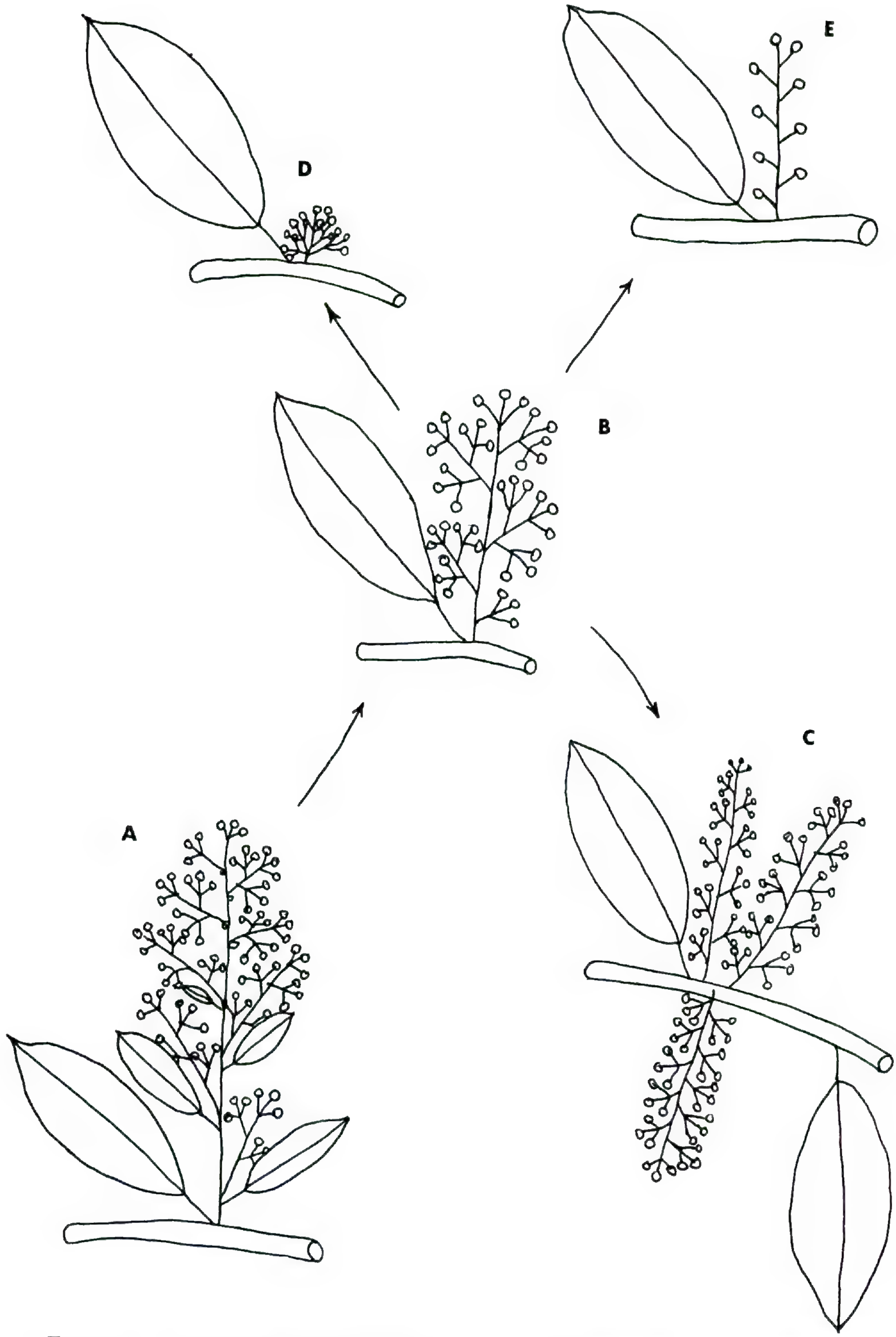


FIGURE 12. Evolutionary trends in inflorescences (diagrammatic).—A. From *Maripa* sect. *Maripa*.—B. From *M.* subsect. *Mouroucoa, Dicranostyles, and Lysiostyles*.—C. From *Dicranostyles*.—D. From *M.* subsect. *Yacuascae*.—E. From *M.* subg. *Ripama*.

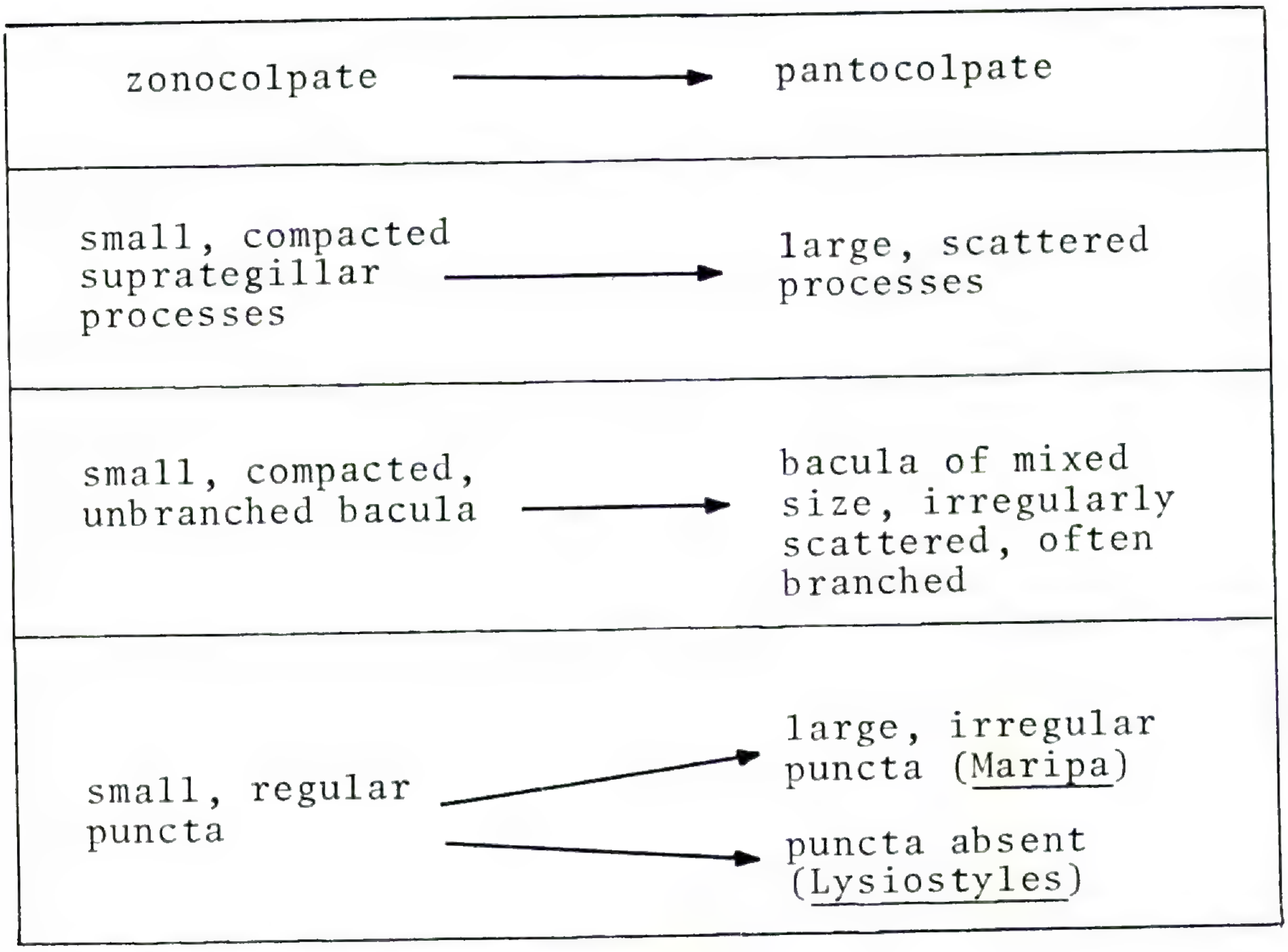


FIGURE 13. Evolutionary trends in pollen.

suprategillar processes to large, scattered processes has accompanied the fusion of bacula. Small, regular puncta are common in zonocolpate grains, while the puncta of pantocolpate grains are larger and irregular in shape. Puncta are apparently absent from *Lysiostyles*. Both irregular, large punta and the absence of puncta appear to be specialized conditions.

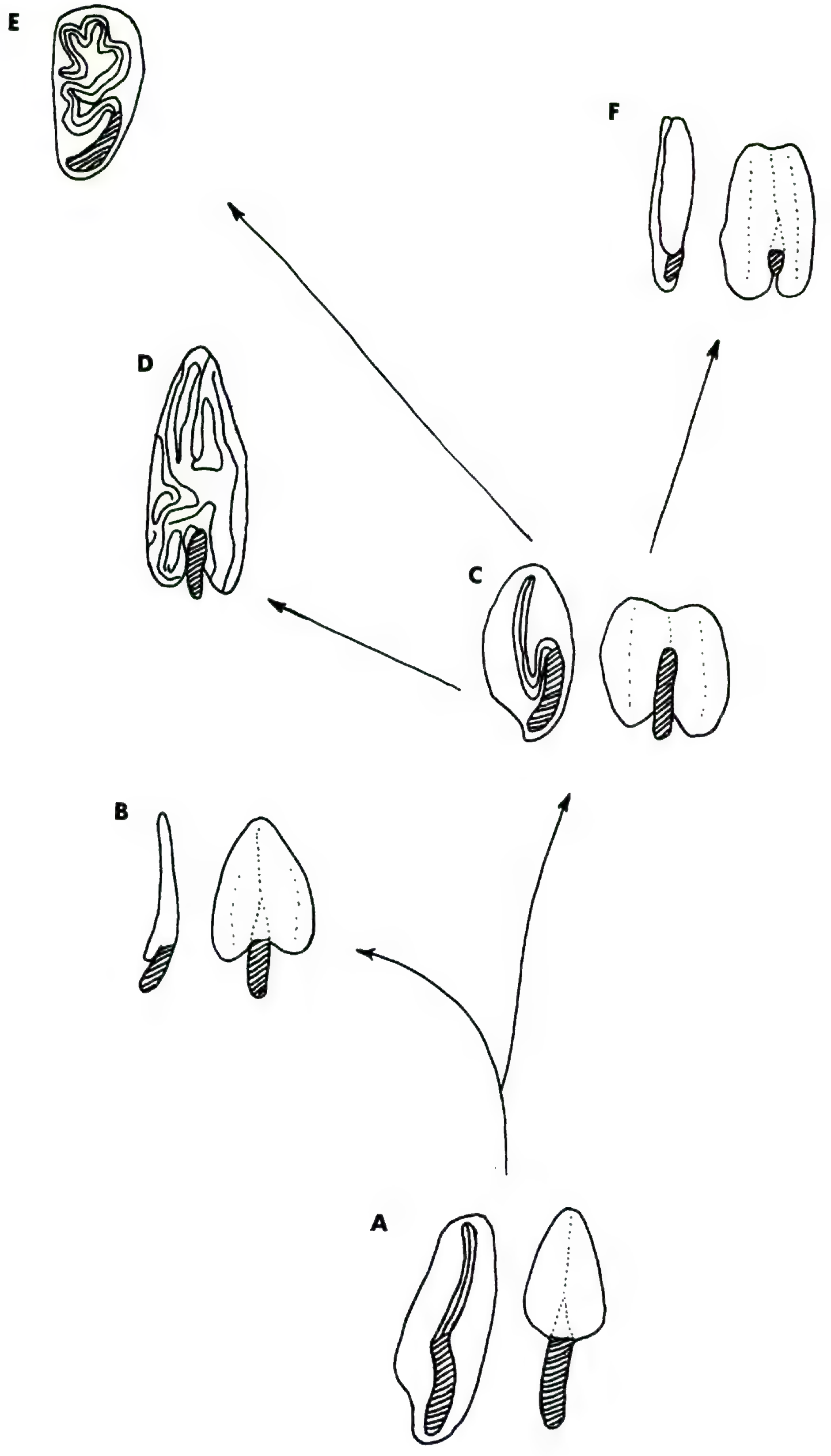
Several of these trends have been discussed by Manitz (1970). My conclusions and data will be compared in detail with Manitz's in another paper.

EMBRYO ONTOGENY-PHYLOGENY FOR THE CONVOLVULACEAE

As the embryo of most species of Convolvulaceae matures, it becomes too large for the enveloping testa. To fit in the existing space the embryo becomes folded along either a longitudinal or latitudinal axis, or both. The folding during ontogeny appears to recapitulate that which occurred during phylogeny. The following definite stages have been determined.

A. Spathulate embryo of *Humbertia* (Fig. 14A). Martin (1946) established that the spathulate embryo is a primitive type. The embryo of *Humbertia* is spathulate, has foliaceous, unfolded cotyledons, and copious endosperm.

B. Spathulate embryo of *Perispermum* (= *Bonamia menziesii*) (Fig. 14B). The cotyledons are larger and more invested around the radicle than in *Humbertia*. The early stages of embryo development in *Jacquemontia* are quite similar to this type, although when fully mature they are as in E.


E
F
D
C
B
A

C. Lati-longiplicate embryo of *Maripa violacea* (Fig. 14C). Note the considerable endosperm remaining in the seed. The embryo has grown so that the surrounding testa has begun to confine it, and folding has begun. Folding is in both directions, neither dominating.

D. Latiplicate embryo of *Bonamia* (sect. *Trichantha*) *trichantha* (Fig. 14D); also found in *Dicranostyles*, *Lysiostyles*, and part of *Erycibe*. Folding is dominantly lateral.

E. Longiplicate embryo of *Ipomoea purpurea* (Fig. 14E). The majority of the genera in the family (*Merremia*, *Bonamia* sect. *Bonamia*, *Jacquemontia*, *Aniseia*, and *Itzaea* were personally examined) appear to have the embryo folded mostly in the longitudinal axis.

F. Latiplicate embryo of *Maripa scandens* (Fig. 14F). The embryos of *Maripa* (excluding *M. violacea*) and part of the genus *Erycibe* are of this specialized type. The radicle is more completely invested than in any other type and reduced to only a rudimentary structure. Instead of the multiple folds found in other genera, the cotyledons have become thickened and are no longer foliaceous. Endosperm is almost absent, remaining only in scanty traces, and a copious perisperm surrounds the seeds. Perisperm is also abundant in the latiplicate embryos of *Erycibe*, *Dicranostyles*, *Lysiostyles*, and reported for *Perispermum* (Degener, 1932).

EVOLUTIONARY TRENDS IN BRANCHED TRICHOMES

The balanced trichomes (Fig. 15A, C) are found in relatively primitive species, and it seems reasonable to assume that they are the prototype for other trichomes. The trichomes found in *Lysiostyles* (Fig. 15C) are perhaps specialized from the other balanced type (Fig. 15A). The unbalanced trichome (Fig. 15B) is common in the tribe and in the family. Indument consisting of this trichome type is normally oriented so that the long branches all point in one direction. The simple trichome (Fig. 15D) occurs sporadically in several other tribes, but only in the most specialized species of *Dicranostyles*.

EVOLUTIONARY TREND FROM PELTATE SCALES TO STELLATE TRICHOMES

Leaves of many species of the Convolvulaceae have simple glandular peltate scales (Fig. 16A, A′). These trichomes occur on the seedling apices of *Maripa* (Austin, in preparation) and in *Convolvulus* (Kennedy & Crafts, 1931). Certain species contain a more complex peltate scale, and several forms may be found on the same flower. There has been a multiplication of cells in the apical portion of the trichomes (Fig. 16B, B′, C). This multiplication has been accompanied by elongation of marginal cells, and reaches its most complex form for the American members of the Erycibeae in *Maripa elongata* (Fig. 16D). Species of *Erycibe* as well as a few species of *Maripa* may be determined by their stellate

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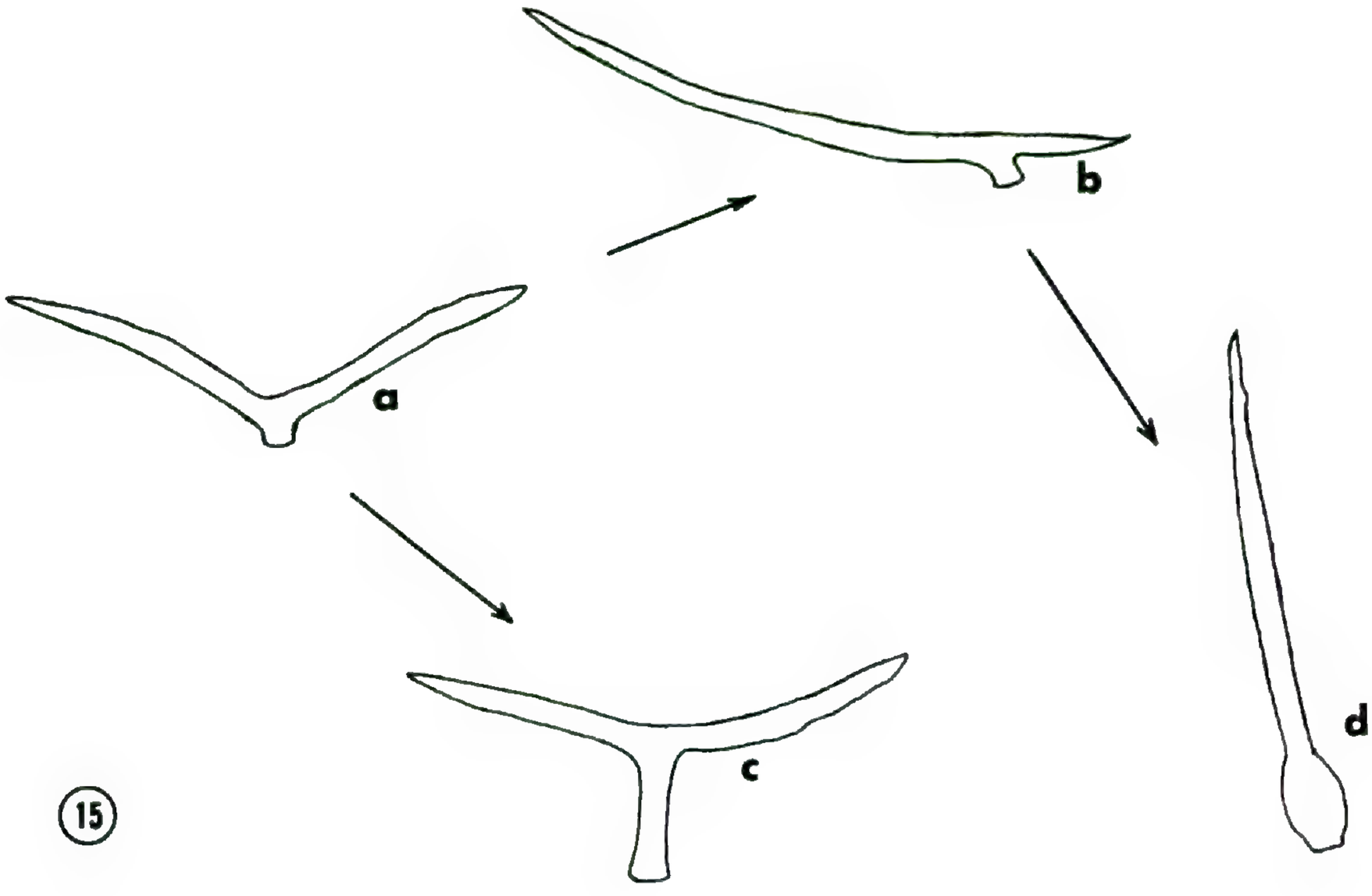
FIGURE 14. Embryo ontogeny-phylogeny for the Convolvulaceae (semidiagrammatic).—A. *Humbertia*.—B. *Perispermum* (= *Bonamia menziesii*).—C. *Maripa violacea*.—D. *Bonamia* sect. *Trichantha*.—E. *Ipomoea purpurea*.—F. *Maripa scandens*.



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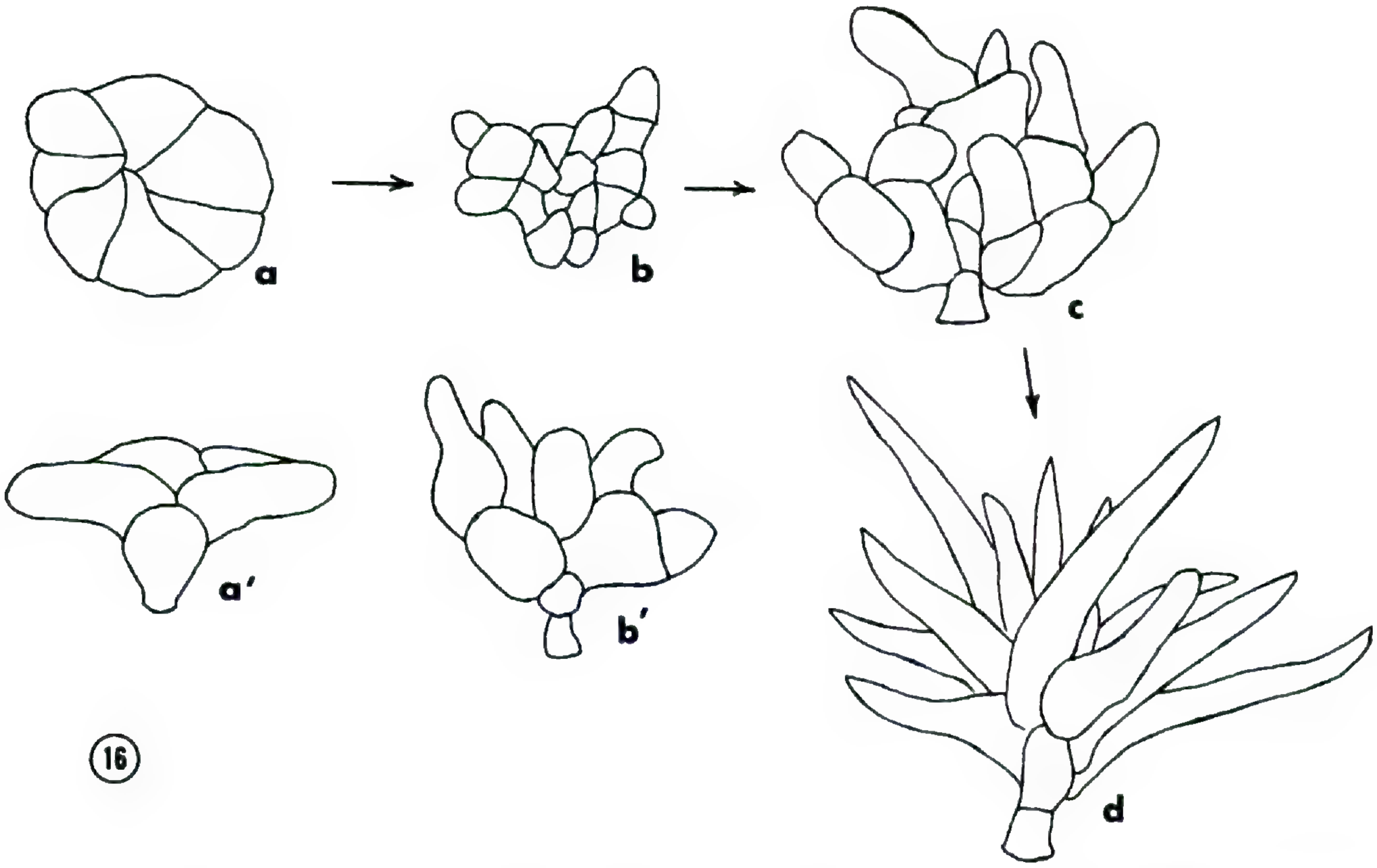

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FIGURES 15–16.—15. Evolutionary trends in branched trichomes.—A. *Maripa janusiana*.—B. *M. violacea*.—C. *Lysiostyles*.—D. *Dicranostyles laxa*.—16. Evolutionary trend from peltate scales to stellate trichomes.—A. Top view, *Maripa violacea*.—A'. Side view, *M. violacea*.—B. Top view, *M. panamensis*.—B'. Side view, *M. panamensis*.—C. Side view, *M. panamensis*.—D. Side view, *M. elongata*.

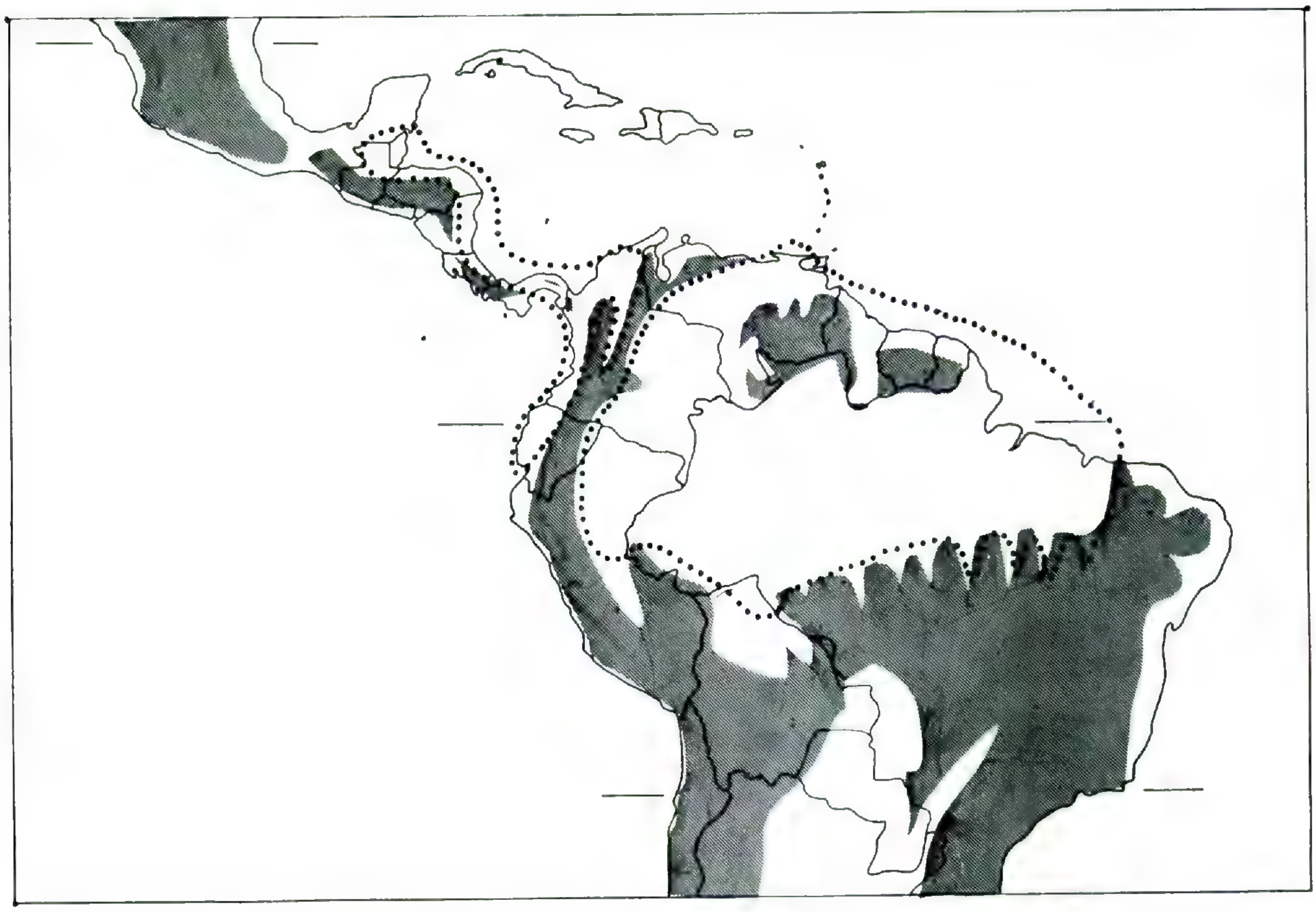


FIGURE 17. Elevation of the geographical area in which members of the American Erycibeae occur. Cross-hatched area above 350 m (1000 feet), white area below 350 m. Distribution of the tribe Erycibeae within the dark line.

trichomes. Stellate trichomes are absent from most species of *Maripa* and all species of *Dicranostyles* and *Lysiostyles*.

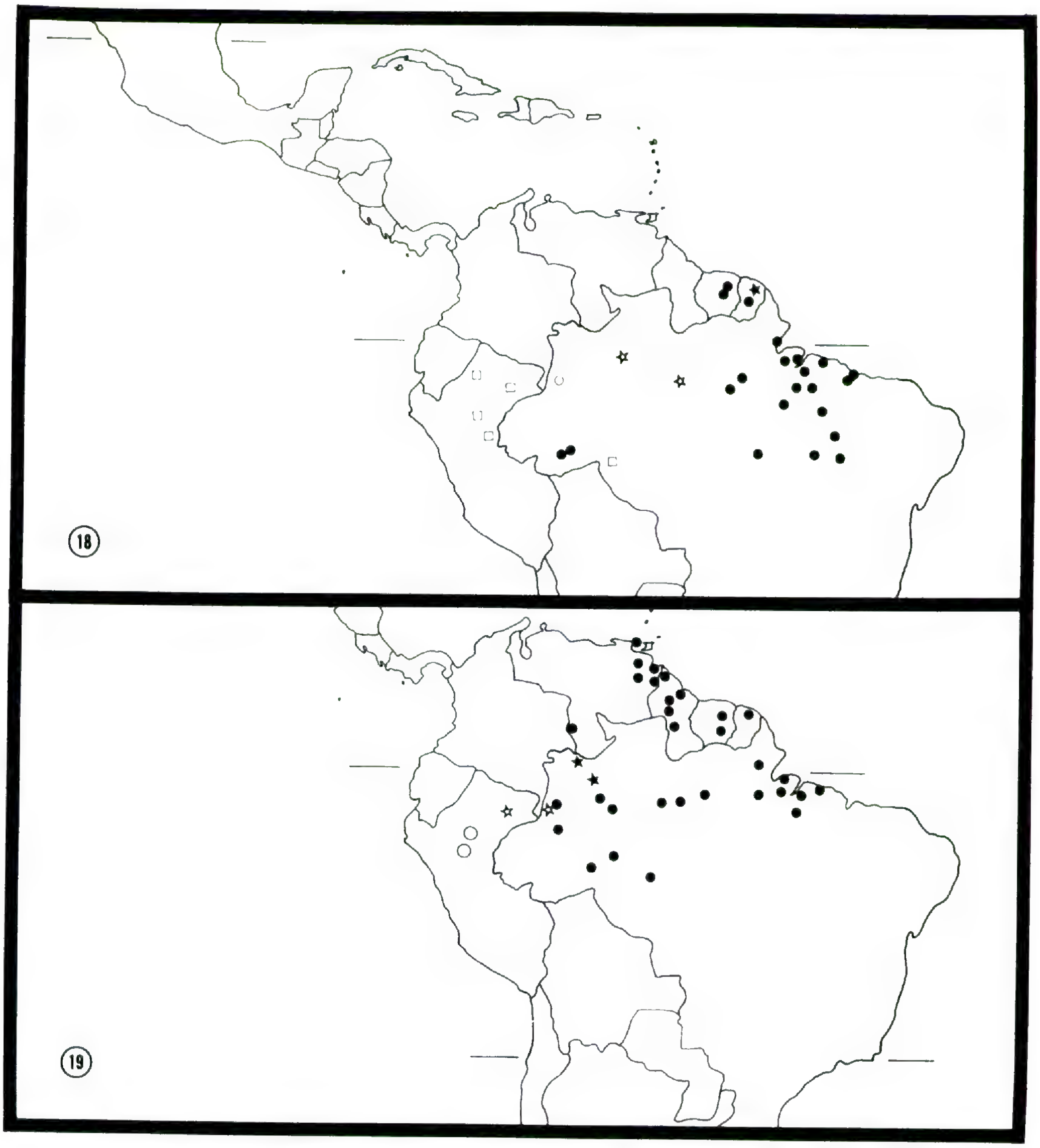
DISTRIBUTION

The American members of the tribe Erycibeae are found from Petén Province, Guatemala, and Stann Creek District, Belize, south to El Beni Province of Bolivia. The range is from about 18° north latitude to about 12° south latitude. Within this area the plants occupy the terrain mostly below about 350 m in elevation (Fig. 17). Plants are occasionally collected above this, some up to 1500 m, but the majority of species are concentrated in the lowlands.

Maripa subg. *Ripama* (Fig. 18) is concentrated in the Guiana lowlands and along the Amazon River. Members of this subgenus occupy the most southern part of the range for the genus. This subgenus has been collected as far north as Jodensavanna in Surinam, as far east as Ilha de São Luiz de Maranhão in Brazil, and up the Tocantins River valley to the vicinity of Carolina in the State of Goiás, Brazil.

From the eastern part of the range the subgenus extends west to the States of Rondonia and Acre in Brazil, and the Departments of Loreto and Amazonas in Peru. In the western part of the range the subgenus is found only as far north as Tapurucoara (Barcelos), Manaus, and São Paulo de Olivença in Brazil.

The tautonymic subgenus of *Maripa* is distributed over a much larger area,

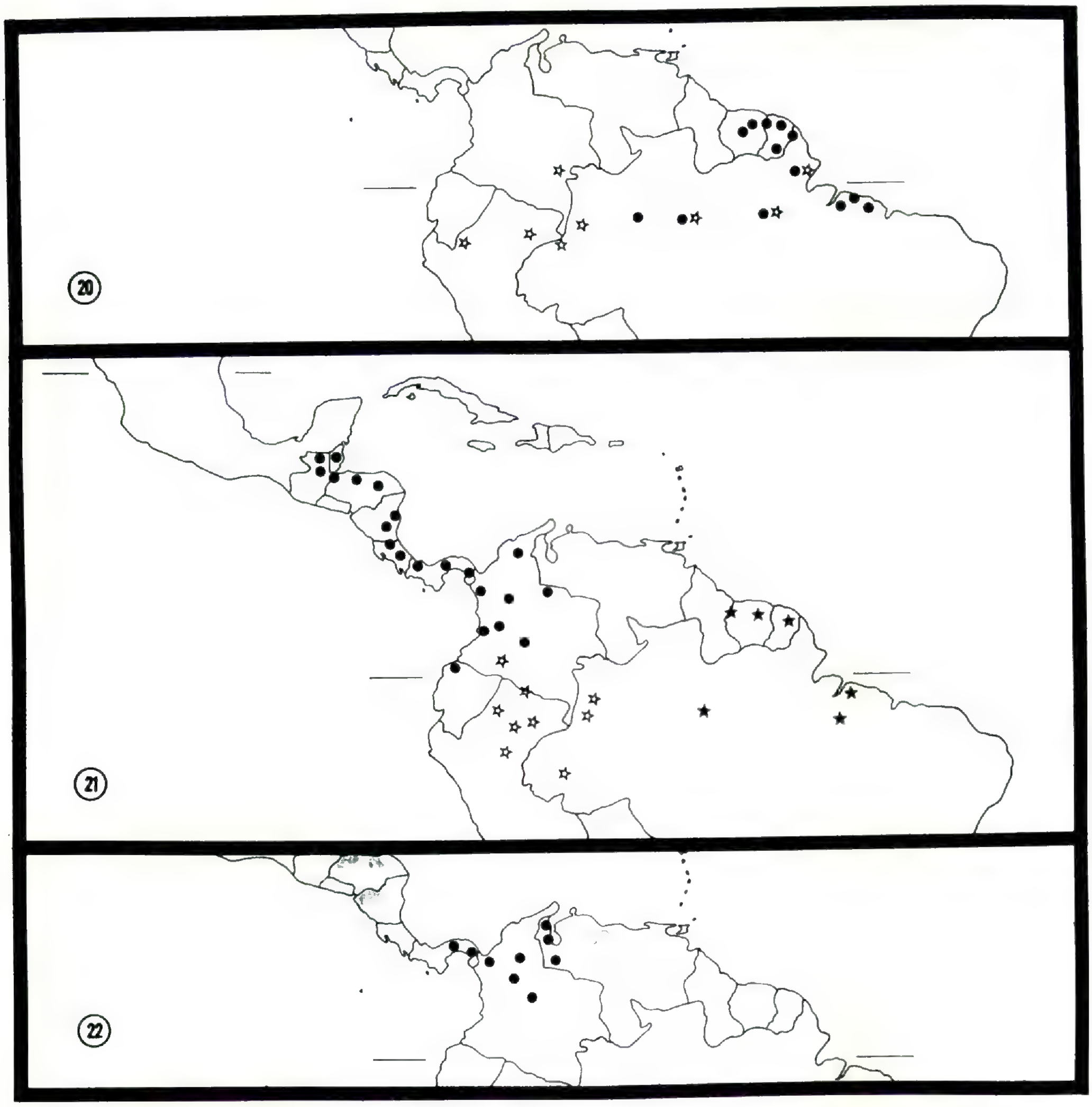


FIGURES 18–19.—18. Distribution of *Maripa* subg. *Ripana*.—● *M. reticulata*.—○ *M. reticulata* var. *rugosa*.—★ *M. longifolia*.—□ *M. axilliflora*.—19. Distribution of *Maripa* sect. *Maripa*.—● *M. scandens*.—○ *M. williamsii*.—☆ *M. janusiana*.—★ *M. densiflora*.

extending from the Amazon River Basin north to Belize and Guatemala in Central America. It is larger than the subg. *Ripama* and is separable into two sections and three subsections.

Section *Maripa* (Fig. 19–20) occurs chiefly north of the Amazon River, although *M. scandens* is widely spread from the Venezuelan Peninsula de Paria west of Trinidad almost to São Luiz de Maranhão in the east and west into the Rio Madeira basin and the Brazil-Peru border.

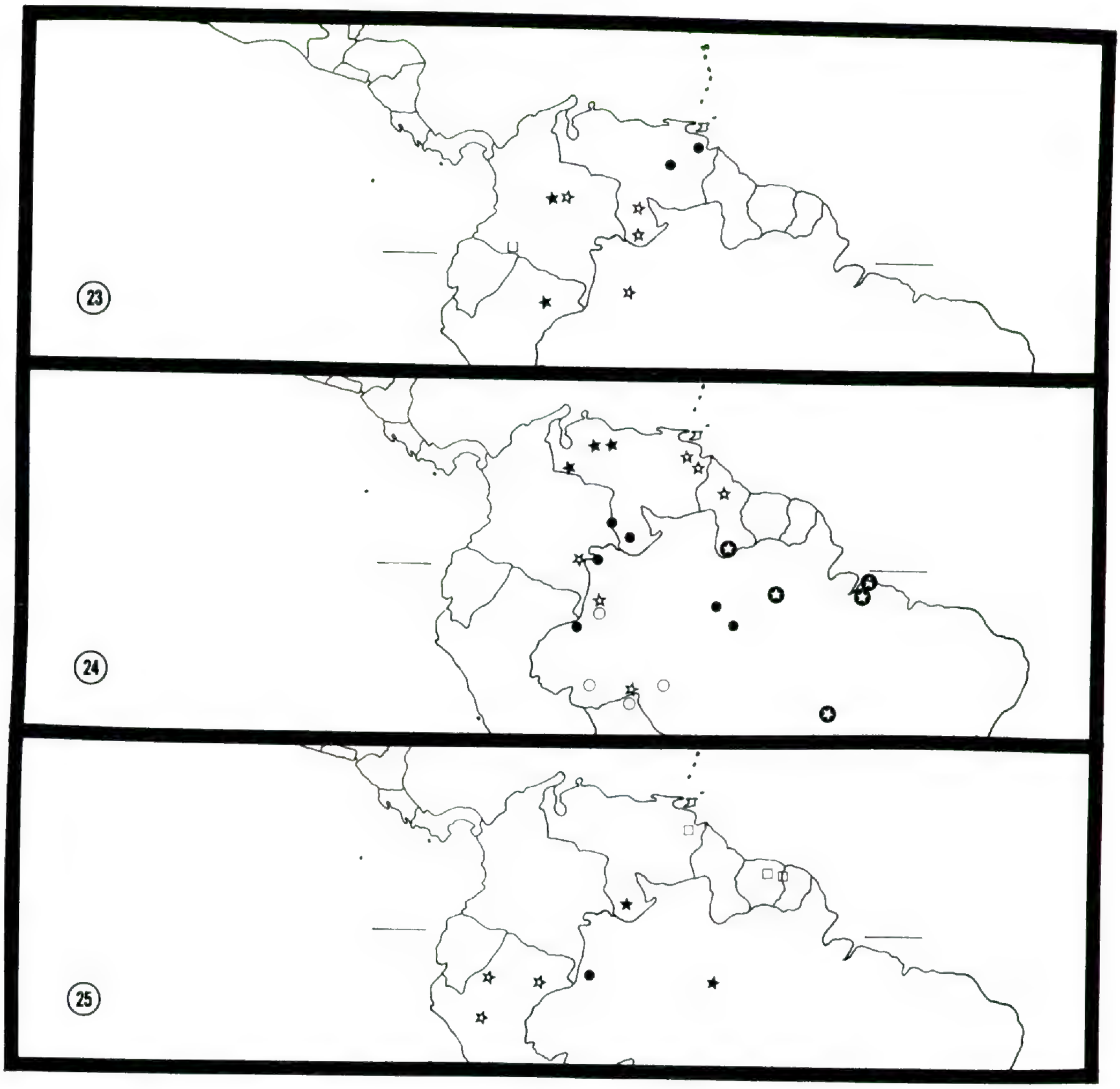
Section *Mouroucoa* is more widespread and more diverse. Its three subsections occur from Belém and the Rio Mojú (State of Pará) west to the State of Acre in Brazil, and the Department of Loreto in Peru. From this southern area



FIGURES 20–22.—20. Distribution of *Maripa* sect. *Maripa*.—● *M. glabra*.—☆ *M. paniculata*.—21. Distribution of *Maripa* subsect. *Mouroucoa* and subsect. *Melofructae*.—★ *M. violacea*.—☆ *M. peruviana*.—● *M. nicaraguensis*.—22. Distribution of *Maripa* subsect. *Melofructae*.—○ *M. stellulata*.—● *M. panamensis*.

the section extends to Central America. Subsection *Mouroucoa* (Fig. 21) is found only on the southern and eastern sides of the Guiana Plateau in Guyana, Surinam, French Guiana, and Pará and eastern Amazonas in Brazil. Subsection *Melofructae* (Fig. 21–22) is found in northwestern South America from the State of Acre in Brazil and the Department of Loreto in Peru, north into Colombia, western Venezuela, and through Central America almost to the Yucatán Peninsula. Subsection *Yacuascae* (Fig. 23) is found only in the upper Amazon and Orinoco River basins of Colombia, Venezuela, Peru, and Brazil. The majority of species occur in river valleys leading up the highlands surrounding the river basins.

The genus *Dicranostyles* has a range similar to that found in *Maripa*, but it is less widespread, being absent from Central America. Subgenus *Dicrano-*

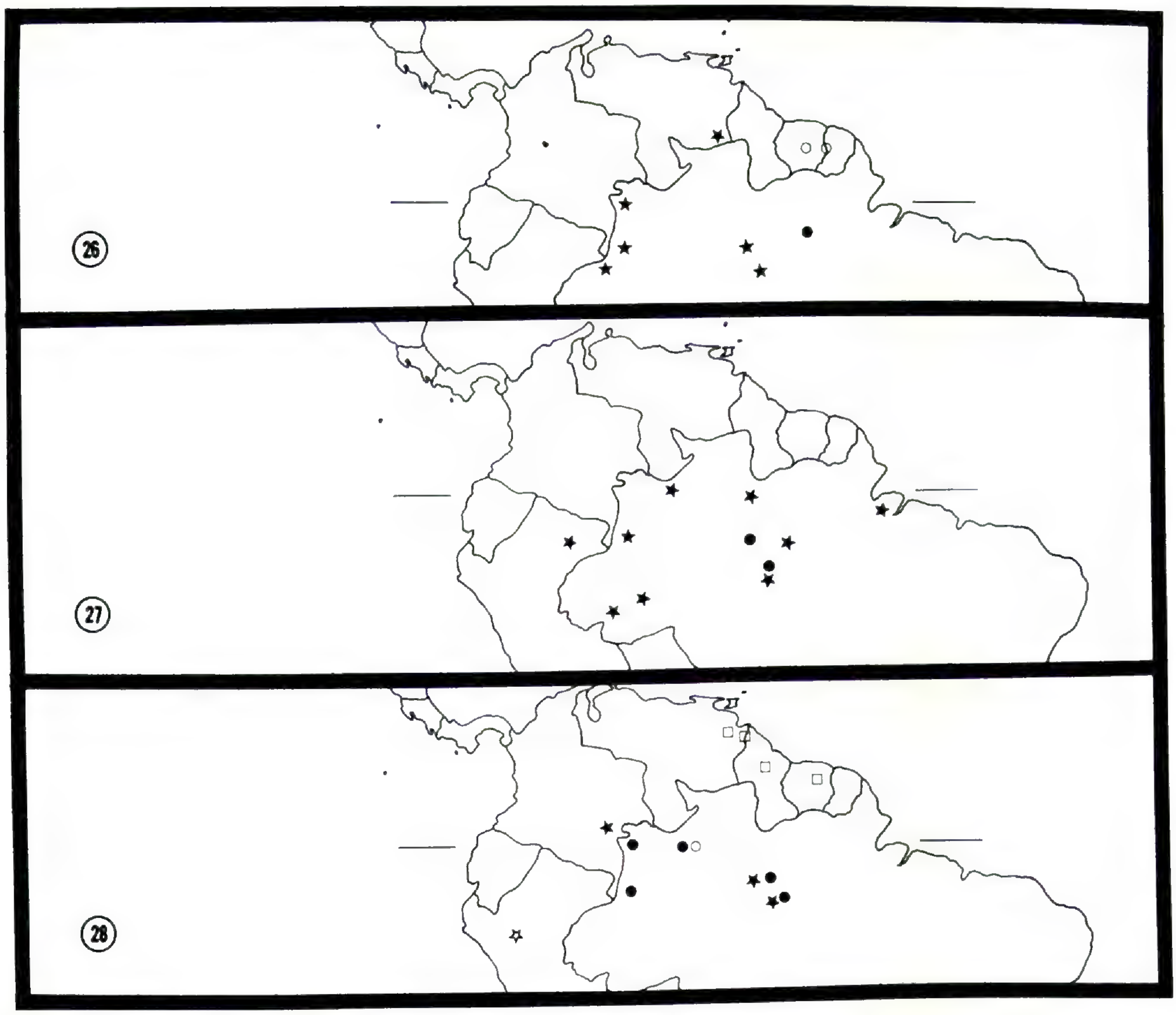


FIGURES 23–25.—23. Distribution of *Maripa* subsect. *Yacuascae*.—● *M. repens*.—☆ *M. pauciflora*.—★ *M. fasciculata*.—□ *M. putumayana*.—24. Distribution of *Dicranostyles* subg. *Dicranostyles*.—★ *D. costanensis*.—● *D. scandens*.—☆ *D. ampla* var. *ampla*.—✪ *D. ampla* var. *castanea*.—○ *D. ampla* var. *attenuata*.—25. Distribution of *Dicranostyles* subg. *Dicranostyles*.—☆ *D. sericea*.—★ *D. densa*.—● *D. solimoesensis*.—□ *D. guianensis*.

styles is found from the Sierra Imataca near the mouth of the Río Orinoco in Venezuela, east to Pará, southwest to Rondonia and Acre in Brazil and into El Beni, Bolivia, the Departments of Loreto and Amazonas in Peru, and north to the southern side of the Coastal Cordillera in Venezuela (Fig. 24–26).

Subgenus *Kuhlmanniella* has a more restricted range with the majority of species being concentrated in the upper Amazon area (Fig. 27–28) of Brazil and Peru. The easternmost collection of the subgenus is from the town of Breves on the Ilha de Marajó at the mouth of the Amazon River. The Rio Negro basin has more species of this subgenus than any other area.

The genus *Lysiostyles* has the most restricted range of any member of the tribe in the New World. This genus is found only on the northern side of the



FIGURES 26–28.—26. Distribution of *Dicranostyles* subg. *Dicranostyles*.—★ *D. longifolia*. —● *D. villosus* var. *villosus*.—○ *D. villosus* var. *lasiocalyx*.—27 . Distribution of *Dicranostyles* subg. *Kuhlmanniella*.—★ *D. holostyla*.—● *D. falconiana*.—28. Distribution of *Dicranostyles* subg. *Kuhlmanniella*, and *Lysiostyles*.—☆ *D. mildbraediana*.—★ *D. integra*.—○ *D. globostigma*.—● *D. laxa*.—□ *L. scandens*.

Guiana Plateau in Surinam, Guyana, and near the mouth of the Río Orinoco in eastern Venezuela (Fig. 28).

PHENOLOGY

To fully appreciate the variation in flowering periods in the Erycibeae one must examine the climates of the areas involved. This examination is most easily done with the climate diagrams made according to the method described by Gaussen (1954). Gaussen's method permits an easy and quick evaluation of the variations in temperature and precipitation from month to month. This presentation of climatic data has been most comprehensively accomplished by Walter (1960–1967).

Examination of the climates in the geographical region in which the Erycibeae occur reveals that Köppen's classification (Espenshade, 1960; Trewartha *et al.*, 1961) "Tropical Rainforest" (the coolest month above 64.6°F (18°C)) is divisible into sub-units. Köppen himself recognized the variation within the "Tropical

Rainforest" climate and proposed the two subdivisions "Af" (moist throughout the year: no month with less than 2.4 inches of rain) and "Am" (monsoon subtype with a short moderately dry season, usually at the time of low sun, or winter). These subclimates are essentially identical to those that Galvão (1967) later designated "Thermaxeric (Equatorial)" and "Subthermaxeric (Tropical)" for Brazil. The distinction between them is that the Af or Thermaxeric regions are essentially without a dry season, while the Am or Subthermaxeric areas have a notable dry period.

Most parts of Central America and northwestern South America, although designated Af by Köppen, actually have a short dry season occurring between January and June. In the Af climate of the upper Amazon region, however, the climate conforms with Köppen's Af definition in having no appreciable dry season, rainfall being distributed almost equally throughout the year. A small area in eastern Venezuela and northwestern Guyana has a similar climate.

The lower Amazon, as its Am designation implies, has a definite dry season which occurs during the wet season of Central America and Northwestern South America (July to December).

To apply formal technical names and attempt detailed explanations of these three climatic areas is beyond the scope of this study. Instead, they will be referred to as "Central American," "lower Amazonian," and "transitional" climates. The transitional areas, those with no dry season, appear to exist because the wet-dry periods of the Central American and lower Amazonian climates are out of phase, one providing moisture when the other is dry.

These climates are associated with different flowering periods within the Erycibeae. When all species of *Maripa* are graphed together, the flowering period is bimodal. If, however, the subgeneric taxa are examined separately, each is found to be monomodal (Fig. 30).

In the lower Amazonian climate (Fig. 29), for example, *Maripa* subg. *Ripama* and *M.* subsect. *Mouroucoa* flower during the wet season and have peaks in February and April, respectively, *i. e.* one month before and one month after the vernal equinox. *Maripa* sect. *Maripa* in the same area produces flowers at the end of the dry season and peaks during November, one month before the winter solstice.

Maripa subsect. *Melofructae* in the Central American climate produces flowers during the same month as the related subsect. *Mouroucoa* (April), even though April is the beginning of the dry season in Central America rather than the wet season as in the lower Amazon.

Flowering is more irregular in the transitional climates, but species growing there tend to flower during the same part of the year as their relatives in other climatic regions. For example, plants of subsect. *Melofructae* and *Yacuascae* have slight peaks during April. Members of *M.* sect. *Maripa* in the western transitional zone conform even more to the pattern of related lower Amazonian plants, having definite flowering peaks during November. There are occasional plants in all species which flower out of synchrony with most members of the population, and these individuals usually do so near the months of April, June, or November.

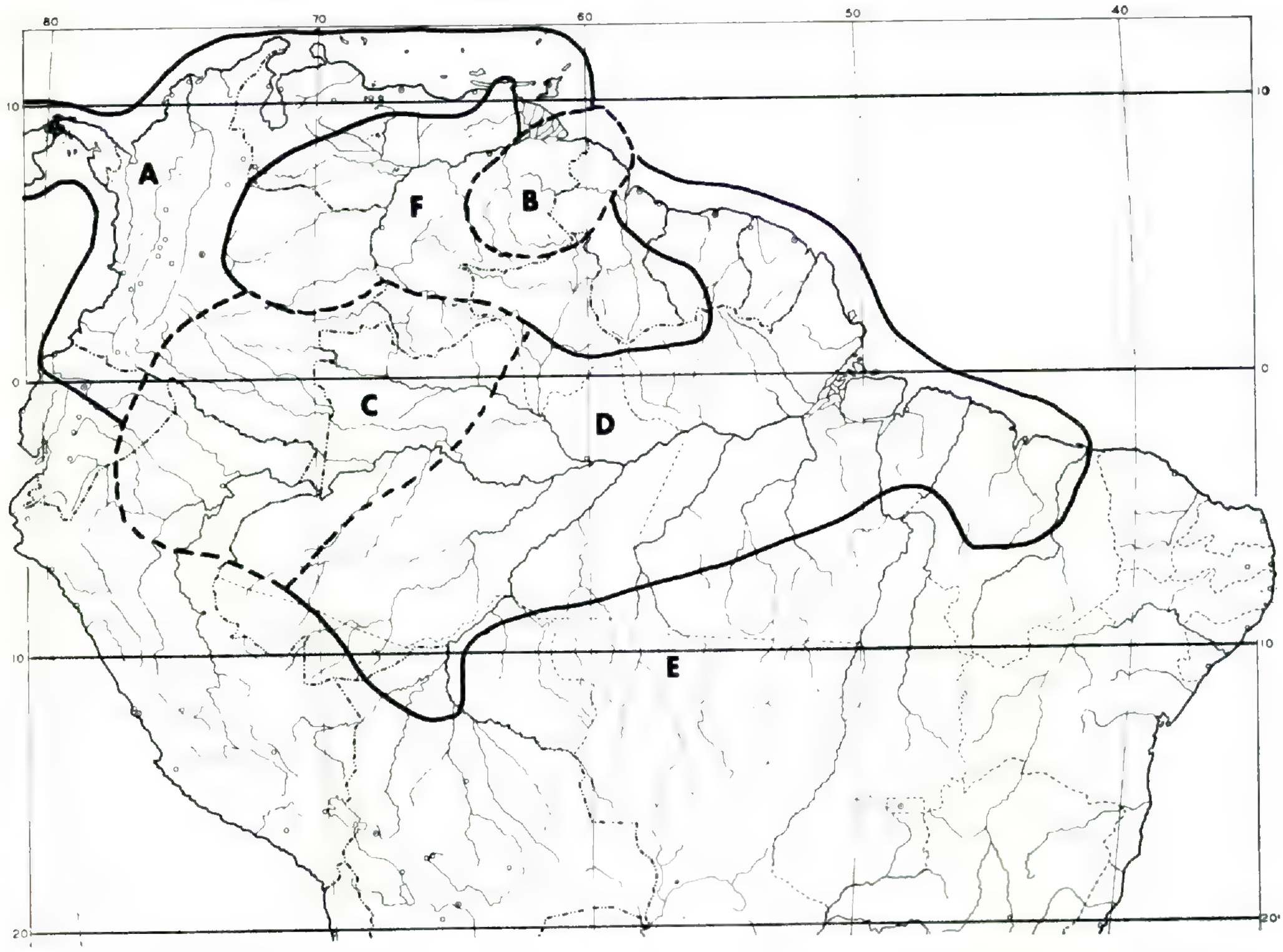


FIGURE 29. Climatic regions within which the American Erycibeae occur. There are three different climatic regions in which the tribe occurs: A. The Central American type with a short dry season in the first six months of the year. B–C. The two transitional regions with essentially no dry season. D. The lower Amazonian with a short dry season in the last six months of the year. Members of the tribe are absent from E, the Planalto of Brazil with a pronounced dry season in the middle of the year, and F, the Llanos of Venezuela, Colombia, and Guyana with a pronounced dry season extending for several months.

It is interesting to compare related Old World genera with *Maripa* with respect to flowering periods (Fig. 30–31). *Erycibe* is morphologically similar to *M.* subg. *Ripama*, and both flower during the first six months of the year. Similarly, *Humbertia* is morphologically much like *M.* sect. *Maripa*, and both flower during the last six months of the year. Both *Erycibe* and *M.* subg. *Ripama* are similar in flowering mostly during the wet season, while *Humbertia* differs from *M.* sect. *Maripa* in flowering during the wet season.

The two subgenera of *Dicranostyles* do not flower in distinctly different periods as do the subgeneric taxa of *Maripa*. Both subgenera of *Dicranostyles* have flowering periods which peak near the equinoxes. While they occur close to these events, they are slightly out of phase: *D.* subg. *Kuhlmanniella* peaks in September and coincides with the autumnal equinox, while subg. *Dicranostyles* does not peak until November. Both show smaller peaks during the vernal equinox in March, although the peak for subg. *Dicranostyles* is much more pronounced.

Within the subg. *Dicranostyles* there is a tendency for plants to continue flowering at the end of the dry season. The species *D. costanensis* and *D.*

FIGURES 30–31. Flowering periods of genera in the Convolvulaceae. The vertical axis on the bar graphs indicates the numbers of collections made of plants flowering in the various months. The months are designated by their initial letter on the horizontal axis of the graphs. —30. The tribe Erycibeae.—31. Representative genera of Convolvulaceae. [Data for *Convolvulus* were taken from Sa'ad (1967), for *Bonamia* from Myint and Ward (1968), for *Humbertia* from Pinchon (1945, 1951). All other data were taken from herbarium specimens.]

scandens occur in the northwestern part of the upper Amazon and the northern side of the Llanos. These species are closely allied, and both peak more heavily during the first three months than most other species in the subgenus. These two species and the related Peruvian mountain valley species *D. sericea* account for most of the January–March peak in subg. *Dicranostyles*. The remaining species in this subgenus and especially those farther east peak heavily around November.

Lysiostyles peaks during June and July, but plants have been collected in September, November, and December. This genus is restricted to the lowland Guianas, where it flowers mostly during the end of the wet season.

There is a correlation between flowering periods and subgeneric classification of *Maripa*. The flowering of these groups in different months reduces the possibility of cross pollination and undoubtedly contributes to their morphological and genetic divergence.

ECOLOGY

The tribe Erycibeae is mostly confined within the Tropical Rainforest climate of the Köppen (1932) system (Af, Am). In Colombia and Venezuela it has extended into the margins of the Tropical Savanna (Aw) areas largely by following water courses.

While some species of the Erycibeae seem to have preferences for specific

habitats within the wet tropics, all are reasonably tolerant. Most species may be found in all of the three basic local plant associations of the Amazon basin: "terra firme," "várzea," and "igapó." Although these three terms originated and are used only in Brazil, they may apply to formations in all areas of South and Central America which are covered with Tropical Rainforest vegetation (*sensu* Köppen). Sioli (1951), Ducke and Black (1953), Cain *et al.* (1956), Pires (1966), and others have discussed these vegetation types in considerable detail and provided illustrations and definitions of the terms. Yet a review of them is in order for the discussion of density and habitat preferences which follows.

"Terra firme" is the land away from the river basins which is above the level of water during the flood season. Soils of the terra firme are usually of recent origin, rather poor and heavily leached, with a reasonably level surface. Typically they are covered with tall forests. Species composition varies somewhat from region to region, but the physiognomy remains constant.

"Várzea" vegetation is situated on the alluvial areas which are subject to periodic flooding by the rivers. The lands are moist at least during the period of flooding in the wet season. There is more organic material in the soils of the várzea, but the high water content prevents heavy agricultural usage. In spite of the high moisture content, the várzea soils are those most commonly cultivated. The forest of the várzea is lower than that of the terra firme and has more palm species, at least in the estuary region (from the Rio Xingú to the mouth of the Amazon).

While the várzea and the "igapó" are vegetationally and edaphically distinct, many local natives use the two terms interchangeably. The term igapó is more correctly applied to areas where the soils are permanently charged with a high water content and often covered with surface water which is slow moving or standing. The igapó is normally between the várzea and the terra firme, and, since the waters are standing or almost standing, they become transparent or dark in color due to silt loss and an increase in dissolved chemical content. Acidity is generally very high. The forest of the igapó is more or less intermediate in height between the várzea and terra firme, and, like the terra firme, palms are rare.

On the lands of IPEAN in Belém, Brazil, there are two ecological reserves staked into quadrants and carefully mapped: Mocambo and APEG. Several reports have been made on the phytosociology of these reserves, but none contains data on the tribe Erycibeae. In fact, few phytosociological reports contain ecological data on vines. During the summer of 1969 I visited these reserves and collected certain information on the Erycibeae growing there.

Mocambo is an island of terra firme surrounded by igapó. The forest on this island is apparently mature and perhaps has never been cut. The actual area staked and divided into quadrants is 250 by 420 m or about 5.5 hectares. The soils of this area are typical of similar areas in the Amazon basin. Falesi (unpublished) has made a survey of the soils and found yellow latosols, concretionary laterites, hydromorphic laterites, moist gleys, bog or half-bog, and semi-gley. The laterites and latosols are terra firme soils, while the others are igapó types. In this area six mature individuals of *Maripa* (5 of *M. glabra* and 1 of *M.*

reticulata) and one mature individual of *Dicranostyles* (*D. ampla* var. *castanea*) were found. The density of Erycibeae on this 5.5 hectare tract was about one mature *Maripa* per 17,500 square meters and one mature *Dicranostyles* per 105,000 square meters. The dominant species was *M. glabra*. One individual just outside the boundary was figured in the density ratios.

In an area known as Kilometer 15 and not set up with quadrants, I found seventeen plants of *M. glabra* (about half were mature individuals) in less than two kilometers. Only one of these plants was growing on the border of the terra firme in an igapó; the remainder were on terra firme. The plants were growing in a "capoeirão" or old cut-over forest. The canopy was closed so that the new forest had been growing for quite some time.

The "Várzea do Aurá" (APEG) is a várzea which is covered by a mature, undisturbed forest at the margins of the Rio Guamá and Rio Aurá. The area which has been staked is 500 by 2000 m or about 100 hectares. The soils of this várzea are basically moist gley types (Falesi, unpublished). On this várzea five mature individuals of *Maripa* (1 of *M. glabra*, 1 of *M. scandens*, and 3 of *M. reticulata*) were found with one mature *Dicranostyles* (*D. ampla* var. *castanea*). The density of Erycibeae on this 100 hectare plot was about one mature *Maripa* per 200,000 square meters and one mature *Dicranostyles* per 1,000,000 square meters. As on Mocambo the *Dicranostyles* was growing in the same tree as a *M. glabra*.

To derive conclusions from such a small sample is perhaps unwise, but the data suggest that the density of *Maripa* to *Dicranostyles* is about 6:1. The number of herbarium collections of these two genera suggest that *Dicranostyles* is much less common than *Maripa* and that this ratio may be a reasonable approximation. The data above also suggest that *M. glabra* has a preference for the terra firme, while *M. reticulata* and *M. scandens* prefer more moist habitats. These conclusions are also supported by the data from herbarium labels.

Donselaar (1970) examined a number of lianas in Surinam and came to similar conclusions to those derived from my study in Brazil. The Surinam study was conducted on a wide variety of lianas but included five species in the Erycibeae. Donselaar's conclusions agree with my study of *Maripa glabra*, indicating that this species prefers high ground which is not periodically flooded.

The results of my study were not detailed enough to draw many conclusions concerning *Maripa reticulata* and *M. scandens*, but Donselaar has provided more data on these species. He indicated that, in Surinam, *M. reticulata* prefers the plant association he terms "Savanna woods." The data listed below indicate that this species commonly occurs in such a habitat, but it is also found elsewhere. The species is probably most common in savanna areas, as Donselaar indicates. I have seen *Maripa scandens* only along the margins of streams and rivers in Guyana and Brazil. Donselaar found the species most commonly along the margins of forests and woods.

Two species were examined by Donselaar (1970) that I did not have the opportunity to examine ecologically. *Maripa violacea* prefers the high forest in Surinam. That data I gathered from herbarium labels suggest that this species also may be tolerant and occurs in several habitats. Only a few collections of

Dicranostyles guianensis have been made. Donselaar (1970) lists the species from Creek Forest in Surinam.

In an attempt to determine habitat preferences for more species, the following data were compiled from herbarium label.

HABITAT PREFERENCES

1. *Maripa elongata*—terra humida; terra firme; along river; terra arenosa úmido; prope rivulum; capoeirão em logar alto; high forest.
2. *M. reticulata*—beira da floresta ao longo de campo; beira do rio; floresta secundaria; terra firme; border of creek; campo; on terra firme near igapó; várzea; capoeira.
3. *M. axilliflora*—rising ground nr. river; on shores of lake; terra firme.
4. *M. scandens*—margem de um riachinho; silva paludosa non inundabili; terra firme; high forest; river margin; várzea; igapó; edge of seasonal pond; over riverine growth; in mixed forest; in miscellaneous forest; damp humid vale; Jodensavanne; cloud forest; primary forest.
5. *M. densiflora*—várzea; praia baixa; igapó; river islands.
6. *M. paniculata*—upland; terra firme; capoeira fechada.
7. *M. glabra*—high forest; upland; terra firme; várzea; seasonal forest; low forest.
8. *M. violacea*—terra firme in wet sandy virgin forest; igapó; swampy secondary forest; capoeira.
9. *M. nicaraquensis*—thickets; river side; lake shore; swamps; high ridge; mixed forest; gallery forest with cloud forest elements; cloud forest.
10. *M. peruviana*—várzea; terra firme; matorrales; mountain forest; nr. rivers; on beach.
11. *M. panamensis*—rain forest; high forest nr. streams; premontane rain forest; thickets; nr. lakes.
12. *Dicranostyles costanensis*—cloud forests; selva siempreverde.
13. *D. scandens*—beira do rio; várzea; terra firme; ad ripas inundatas.
14. *D. ampla*—terra firme; terre firme beside stream; várzea; igapó.
15. *D. densa*—capoeiras on terra firme; várzea; mature forest.
16. *D. longifolia*—terra firme; margem do rio; high forest; capoeira.
17. *D. holostyla*—terra firme; high forest; beira do rio.

Dispersal

Very little is known of the dispersal mechanisms in the Erycibeae. The sweet perisperm of the fruits is probably related to dispersal, but there are no actual field observations reported. I learned in Guyana (1966) that monkeys and parrots eat the fruits of *Maripa*, and in Brazil (1969) I was told that birds commonly eat fruits of *Maripa*. Oppenheimer (1968) and Duke (1968) have found these same animals utilizing fruits of *Maripa* in Panama.

The sweet perisperm is probably attractive to these animals, which eat away the sweet parts and discard the remaining seeds. In this way the seeds are freed of the surrounding pericarp and are in a more favorable condition to become established, if they fall in a suitable location.

Economic Uses

At present the only use of the American Erycibeae is as an edible fruit by native groups. This use was probably more widespread in the past before large scale acculturation occurred. Castaneda (1961) reports that *Maripa panamensis* in Colombia is called "miel quemada" or burned honey (see also section on common names) and is used by the natives. He says that "the seeds are surrounded by a sweet, blackish, viscous, pasty pulp which is edible and greatly appreciated by the natives, ... but it lacks economic importance because the edible portion is very small in proportion to the remainder of the

fruit and the fruiting is not very abundant" (p. 261). Duke (1967, 1968) lists the fruits of *Maripa* among the edible fresh fruits of Panama. Oppenheimer (1968: 166) states that the white-faced monkey (*Cebus capuchinus*) on Barro Colorado Island, Panama, eats the fruits and that the "brown sticky pulp around the seed is eaten. It tastes like canned prunes."

There are no reports of *Dicranostyles* having similar uses and no common names to suggest that it might be so used. *Lysiostyles*, on the other hand, has been called "melocotón" or peach in Venezuela, and this suggests edible fruits.

Because of the reports of edible fruits, I asked individuals in Iquitos, Peru; Bartica, Guyana; Belém, Brazil; and Dr. Ghillean Prance (personal communication, 1970) asked in Manaus, Brazil. We found no one who was aware of the fruits being eaten.

ETYMOLOGY AND COMMON NAMES

The name "maripa" comes from the Galibi Indian (Carib language stock) word which was used to designate a vine and a palm in the period when Aublet visited French Guiana (1762–1764). Aublet (1775) says that "Cet arbrisseau est appellé Maripa par les Galibis. Le nom de Maripa se donne aussi a une espèce de palmier." What Aublet failed to mention when he established the genus *Maripa* was that he would create the name *Palma maripa* (Aublet, 1775, 2: 974) for the palm he mentioned earlier. Dahlgren (1936) lists the following synonymy for the palm:

Maxmiliana maripa (Aublet) Drude (1882).
Attalea maripa (Aublet) Martius (1847).
Palma maripa Aublet (1775).

The name "maripa" is still applied to the palm in Surinam (John C. Walsh, 1967, personal communication). The use of "maripa," perhaps both the palm and the vine, was apparently widespread in earlier times because there are towns named "Maripa" in Venezuela, Guyana, and Brazil.

Another name Aublet proposed for plants of concern here was *Mouroucoa*. He states that "mouroucoa-yarana" was the Garipon Indian name applied to this large-flowered plant. Spruce (*in scheda*, 1851) and Martius (1861) reported that the plant was called "murucuarana" or "murucuia-rana" in Manaus and Pará, Brazil, by the Tupí speaking natives. LeCointe (1945) reported later that the plant was then called "maracujá-rana" in Manaus. All these names are different interpretations of the same words, and all are based on words from the Tupí Indian language.

In Tupí, and now in modern Brazilian Portuguese, the Passion Flower (*Passiflora*) is called "maracujá." Each species is given a different "specific epithet," *i. e.* "maracujá-do-rato" (Rat's Passion Flower), etc. The suffix =rana is used in Tupí to indicate that one object may look like another, but is not identical with it. It may be translated as "false." The name that Aublet and the others learned for the plant known currently as *Maripa violacea* may be translated as "False Passion Flower."

The "civilizados," or city and near-city dwellers, in Pará, Brazil, are no longer familiar with many of the terms used by their ancestors. Of the numerous people

questioned in Belém, only one person professed to ever having heard "maracujá-rana" used. Dalton Ferro, now employed by IPEAN in Belém, told me that he had seen the plant once when a friend had pointed it out from a boat in western Pará near Óbidos. Collections of the plant have not been made in that area, so it is not possible to know if the plant Ferro saw was actually *Maripa violacea*.

It is interesting to note that *Maripa peruviana* was known as "mococo-o" by the Huitoto Indians of the Río Zubineta area in Peru. These Indians belong to the Tupí language group, and *M. peruviana* is similar morphologically to *Mouroucoa* (*Maripa violacea*).

In the taxonomic section of this discussion I have created three new subgeneric names within the genus *Maripa*. One of these I have called subg. *Ripama*. This name was derived from the Latin words "ripas," rivers, and "amar," to love, and is intended to convey the preferred habitat of the plants. Another I have called subsect. *Yacuascae*. This name is taken from two Quechua Indian words "yacu," water course or river, and "huasca," vine. The name serves to indicate the general area, western South America, in which the plants may be found, and to suggest that these plants also are found primarily along water courses. All species of *Maripa* require large quantities of water, so these terms are in no way unique to the group of species they describe.

The third group of species I have placed under subsect. *Melofructae* from the Latin "mel," honey, and "fructus," fruit. Although other species have been noted as having a honey-like substance in their fruits, this character is best known for these species.

When Bentham described *Dicranostyles* and *Lysiostyles*, he used names whose meanings are immediately obvious. *Dicranostyles* comes from the Greek root words "di," two, "crano," heads, and "styles," styles. *Lysiostyles* is based on the Greek "lysio" which means splitting. Such characters are not restricted to the species in these genera, but occur in the entire tribe Dicranostyleae *sensu* Hallier (1893).

Within the genus *Dicranostyles* I have recognized two subgenera. The subgenus I have called *Kuhlmanniella* was originally described by Barroso (1945) as a genus distinct from *Dicranostyles*; it is named in honor of the Brazilian naturalist and explorer João Geraldo Kuhlmann.

The following list gives the common names of several species with their derivation and meaning when available.

Maripa subg. *Ripama*

M. reticulata—

"Cipó abacate" (Ilha de São Luiz de Maranhão—*Froes*), Brazilian Portuguese name meaning "vine like the abacate or avocado."

"Cipó brasa" (Belém—*Oliveira*), Brazilian Portuguese name meaning essentially "maripa vine" since "brasa" is a name once given to *Maripa scandens*, *q. v.*

"Baboen-malasi" (Jodensavanne, Surinam—*Vreden*), perhaps a Bush Negro pidgen English name meaning baboon molasses.

sect. *Maripa*

M. scandens—

"Monkey syrup" (Guyana—Persaud, Sandwith).

"Brasa" (Amazonia, Brazil—LeCointe, 1945; Ferreira, 1946, and *Huber*). According to

Ferreira, "brasa" can mean the following: "carvão incandescente; qualidade ou estado de incandescencia; ardor; afogueamento; ira; pl. carvão de lenha miuda; planta da familia Convolvulaceas (*Maripa scandens* Aublet)." [incandescent carbon; quality or state of incandescence; ardor; inflamed; anger; carbon from small wood; plant belonging to the family Convolvulaceae (*Maripa scandens* Aublet)].

M. paniculata—

"Brasa" (Manaus, Brazil—Huber *in scheda*, 1900).

"Moo-se-ree-ha" (Colombia—*Schultes & Cabrera*), a Makuna Indian name (Mashacali language stock?) meaning vine-of-cricket, *fide Schultes & Cabrera.*

M. glabra?—

"Black rope" (Guyana—Rufus Boyan). While I was in Guyana, Rufus Boyan said that there was another plant similar to *M. scandens* which was known locally as "black rope." Although we did not find the plant, he may have referring to *M. glabra.*

sect. *Mouroucoa*

M. violacea—

"Mouroucoa-yarana" (French Guiana—*Aublet*), a Garipon Indian name (Tupí language stock) meaning false Passionflower.

"Murucuarana" or "murucuia-rana" (Brazil—*Spruce*, *Martius*), see discussion above.

"Maracujá-rana" (Manaus, Brazil—LeCointe, 1945), see discussion above.

"Ooneoballi" (Surinam—*Gonggrijp & Stahel*), Arawak Indian name (Carib language stock); meaning unknown.

"Patawana-liane" (Surinam—*Boschbeheer*), a Bush Negro name?; meaning unknown.

subsect. *Melofructae*

M. nicaraquensis—

"Bejuco parra" (Petén, Guatemala—*Aguilar*), a Spanish name meaning literally "vine grapevine."

"Indian Honey" (Middlesex, Belize—*Gentle*).

M. peruviana—

"Mococo-o" (Rio Zubineta, Peru—*Klug*), a Huitoto Indian name (Tupí language stock); meaning unknown.

"Nucnu-huasca" (upper Rio Nanay, Peru—*Williams*), a Quechua name; meaning of "nucnu" unknown, "huasca" means vine.

M. panamensis—

"Miel quemada" (Colombia—Castaneda, 1961), Spanish meaning burned honey.

Dicranostyles subg. *Kuhlmanniella*

D. holostyla—

"Cipó abiú" (São Gabriel, Brazil—*Froes*), a Brazilian Portuguese name apparently alluding to the similarity between the leaves of the "Abiú" or "abieriro" (*Lucuma caimito* Roem. & Schult., Sapotaceae) and the leaves of the vine.

Lysiostyles

L. scandens—

"Melocotón" (Delta Amacuro, Venezuela—*Blanco*), Spanish for peach.

SYSTEMATIC TREATMENT

1. Tribal Relations

When Bentham (1846) described *Dicranostyles* and *Lysiostyles*, their relations within the family seemed clear to him. He said, "they are allied, on one hand, to *Maripa*, on the other to *Erycibe*." Meisner (1869), who studied only American genera, stated that *Dicranostyles* was "genus cum sequente a reliquis

Convolvulaceis corollae aestivatione dissentients et cum *Erycibe* conveniens . . . ; affine *Prevosteae* et *Breweriae* et praecipue *Lysiostyli*, a prioribus corolla subrotata, a posteriore stylo bifido distinctum." Hallier (1893) examined the family thoroughly and followed Meisner in placing *Dicranostyles* and *Lysiostyles* in a tribe distinct from that in which *Maripa* was placed.

In the 80 years since Hallier's revolutionary study of the family, few people have seriously questioned the tribal groupings. Most authors have been concerned chiefly with the level at which species groups should be placed. Some of more noteworthy schemes were produced by Peter, van Ooststroom, and Roberty.

Peter (1897) adopted Hallier's scheme, but more recent editions of Engler's *Syllabus der Pflanzenfamilien* (Engler & Gilg, 1912; Diels, 1936; Melchior, 1964) have followed the unsatisfactory groupings of species he produced earlier (Peter, 1891). Ooststroom (1953) suggested that the generic groups remain much as Hallier proposed but placed them at subtribal rank. Roberty's (1952) first scheme raised almost every genus in the family to subfamilial or tribal rank. He created further complications by ignoring early literature and citing names with the incorrect authorities. Although the schemes proposed by Roberty are among the least natural of those produced for the Convolvulaceae, it is a credit of some magnitude that he was the first person since Bentham to recognize the close relations between *Maripa*, *Erycibe*, *Dicranostyles*, and *Lysiostyles* (Roberty, 1964).

One of the major criteria used in Peter's classification was fruit structure, while Meisner and Hallier stressed both fruit and stylar characters. Considerable new data are now available, using these characters of sufficient importance to warrant several changes in tribal arrangement.

Meisner (1869) established the Dicranostyleae and described it as having "fructus capsularis dehiscens. Styli 2 liveri v. semiconnati (s. stylus bifidus v. bipartitus)." Although Hallier (1893) examined material of *Dicranostyles*, *Lysiostyles*, and *Prevostea* (= *Calycobolus*), he apparently did not see fruiting material for either. Fruiting material has become available for all three of these genera since Hallier's study, and all have indehiscent fruits. The indehiscent fruits, the soft testa, and several other characters require that *Dicranostyles* and *Lysiostyles* be placed in the same tribe with *Maripa*, *Erycibe*, and *Humbertia*. This removes *Dicranostyles* from the tribe it typifies, however, and thus creates the need for a new tribal name. Bentham and Hooker (1873) provided a suitable name, Cresseae. Although as circumscribed by its original authors this tribe included *Wilsonia*, it has been emended below, since this genus is closely allied with the Dichondreae.

Calycobolus (= *Prevostea*), also with indehiscent fruits, has accrescent sepals and a chartaceous fruit wall (Austin, 1971*b*). These characters and others suggest relations with the Poraneae. Two other genera, *Cladostigma* and *Hildebrandtia*, in the Dicranostyleae *sensu* Hallier have accrescent sepals and seem at first to best be placed in the Poraneae. The fruits of the specimens I have examined at the Smithsonian Institution (US), however, all had dehiscent capsules. Both these genera appear to best be considered members of the Cresseae Benth. & Hook. *emend.* D. Austin.

Two groups which share many characters with the Poraneae are the Dichondreae and the Cuscutaceae. These taxa are unique in having indehiscent chartaceous fruit walls, which abciss tardily at the base. The mature fruit shape of the Poraneae and the Cuscutaceae is similar, while the fruits of the Dichondreae are somewhat different; the fruits of *Dichondra* and *Falkia* are mostly reduced to utricles (Tharp & Johnston, 1961). The African genus *Nephrophyllum* has a spiraled embryo which, with fusion of the cotyledons, would be similar if not identical to the embryo of *Cuscuta* (Richard, 1850, *tab. 76*). *Wilsonia*, an Australian genus, has been separated as a monotypic tribe by several authors, but this seems unwarranted. The main criterion for separation seems to be the gamosepalous calyx. Yet this character is shared by *Dichondra* and *Falkia*, although the fusion is not as complete in these genera.

Within the Dicranostyleae *sensu* Hallier there remains one other genus without apparent close relations, namely *Evolvulus*. The pantocolpate pollen, campanulate corolla, and the base chromosome number of $n = 12$ in this genus suggest close relations with *Convolvulus* and *Jacquemontia*. The unusual stylar and stigma characters of *Evolvulus* are similar to those in *Polymeria*, which is endemic to the Australian area. The relations between *Evolvulus* and *Polymeria* should be studied more thoroughly.

A close examination of the genera in the Convolvuleae suggests that *Convolvulus*, *Calystegia*, *Evolvulus*, *Jacquemontia*, and *Polymeria* form a closely related group which differs from the remainder of the genera placed together by Hallier. Cytological data, corolla shape, stylar characters as well as discussions with K. R. Robertson (see Robertson, 1970) have further convinced me that these five genera should be separated from the "Merremioid" segment. Without a detailed study, however, I am not prepared to make a formal transfer and create a new tribal name for the "Merremioid" segment.

SUMMARY OF TRIBES

1. ERYCIBEAE (Endl.) Hall. f., Bot. Jahrb. Syst. 16: 576. 1893.

For synonymy and description see taxonomic section.

General included: *Maripa* Aublet, 1775; *Humbertia* Lam., 1786; *Erycibe* Roxb., 1798; *Dicranostyles* Benth., 1846; *Lysiostyles* Benth., 1846.

2. CRESSEAE Benth. & Hook., Gen. Pl. 2: 868, 1873, pro parte, emend. D. Austin.

Convolvuloideae-Hildebrandtieae Peter *in* Engler & Prantl, Nat. Pflanzenfam. 4(3a): 19–20. 1891.
Dicranostyleae (Meisn.) Hall. f., Bot. Jahrb. Syst. 16: 569. 1893, pro parte maiore.
Cresseae Roberty, Candollea 14: 28. 1952, *nom. illeg.*
Neuropeltidae Roberty, Candollea 14: 28. 1952.
Dicranostylinae v. Ooststr., Fl. Males. 4: 389. 1953, pro parte maiore.

Lianas, *shrubs*, suffrutescent shrubs, and herbs. *Leaves* large to small, often cordate, elliptical or ovate, coriaceous or membranaceous. *Flowers* small to large, in lateral dichasia, 1–∞-flowered, less commonly in compound-panicles; sepals ovate, obovate or lanceolate, not accrescent, equal or unequal, coriaceous or membranaceous; styles bifid or 2 and free. *Fruits* dehiscent, medium to small,

subligneous to subcoriaceous; seeds medium to small, occasionally surrounded by perisperm, the testa, if coriaceous, pilose with long trichomes, otherwise hard, ligneous and glabrous or pubescent, the cotyledons longiplicate or latiplicate (in *Bonamia* sect. *Trichantha*).

Leaf structure mostly aequifacial; spongenchyma, if present, of small unbranched cells; stomata with 3, rarely 2, accessory cells; trichomes dibrachiate, glandular indument with usually ellipsoid heads, horizontal and vertical septa, chambered; fibrovascular bundles often with idioblasts scattered among the regular network of veins, the bundles often with sclerenchymatous sheaths; glandular cells solitary, occasionally in phloem or mesophyll, rarely in cotyledons.

Pollen 3-colpate or pantocolpate.

Genera included: *Cressa* L., 1753; *Bonamia* DuPetit-Thouars, 1804; *Neuropeltis* Wall., 1824; *Stylisma* Raf., 1825; *Seddera* Hochst., 1844; *Itzaea* (Standl.) Standl. & Steyerm., 1944; ?*Neuropeltopsis* v. Ooststr., 1964.

3. Poraneae Hall. f., Bot. Jahrb. Syst. 16: 574, 1893.

Lianas, or shrubs. *Leaves* medium to large, often cordate, herbaceous to chartaceous. *Flowers* mostly small, in racemose clusters or less often compound-panicles; sepals oblong to ovate, the 3 outer, or rarely all, strongly accrescent around the fruit, chartaceous to membranaceous; styles entire or less commonly bifid. *Fruits* indehiscent, mostly small, with a membranaceous to chartaceous wall; seeds medium to small, perisperm absent, the testa hard-coriaceous, the cotyledons longiplicate (exclusively?).

Leaf structure predominantly bifacial; spongenchyma not described; stomata with 2, rarely 3, accessory cells; trichomes dibrachiate, rarely simple, the glandular indument capitate, often strongly septate below, radiate 4- rarely many-celled, occasionally of 2 types: sparsely transversely septate or with many transverse septa; fibrovascular bundles not described; glandular cells absent, solitary in the middle of the mesophyll, or within parenchyma cells near the larger nerves.

Pollen 3-colpate, pantocolpate, or pantoporate (*Cardiochlamys*).

Genera included: *Porana* Burm., 1768; *Calycobolus* Willd., 1819; *Cardiochlamys* Oliver, 1883; *Rapona* Baillon, 1891; *Dipteropeltis* Hall. f., 1898; *Metaporana* N. E. Br., 1914.

Without further study I shall not attempt to characterize the following tribes. Hallier (1893) has given a fairly complete description of each; I shall only list the genera that my study suggests would best be included in each tribe.

4. Convolvuleae (Choisy) Choisy *in* DC. Prodr. 9: 325. 1845, *sensu restricto*.

Genera included: *Convolvulus* L., 1753; *Evolvulus* L., 1762; *Calystegia* R. Br., 1810; *Polymeria* R. Br., 1810; *Jacquemontia* Choisy, 1834.

5. "Merremioids"

Genera included: *Merremia* Dennst., 1818, *emend.* Hall. f., 1893; *Aniseia* Choisy, 1834; *Operculina* S. Manso, 1836; *Hewittia* Wight & Arn., 1837; *Iseia* O'Donell, 1953; *Tetralocularia* O'Donell, 1960.

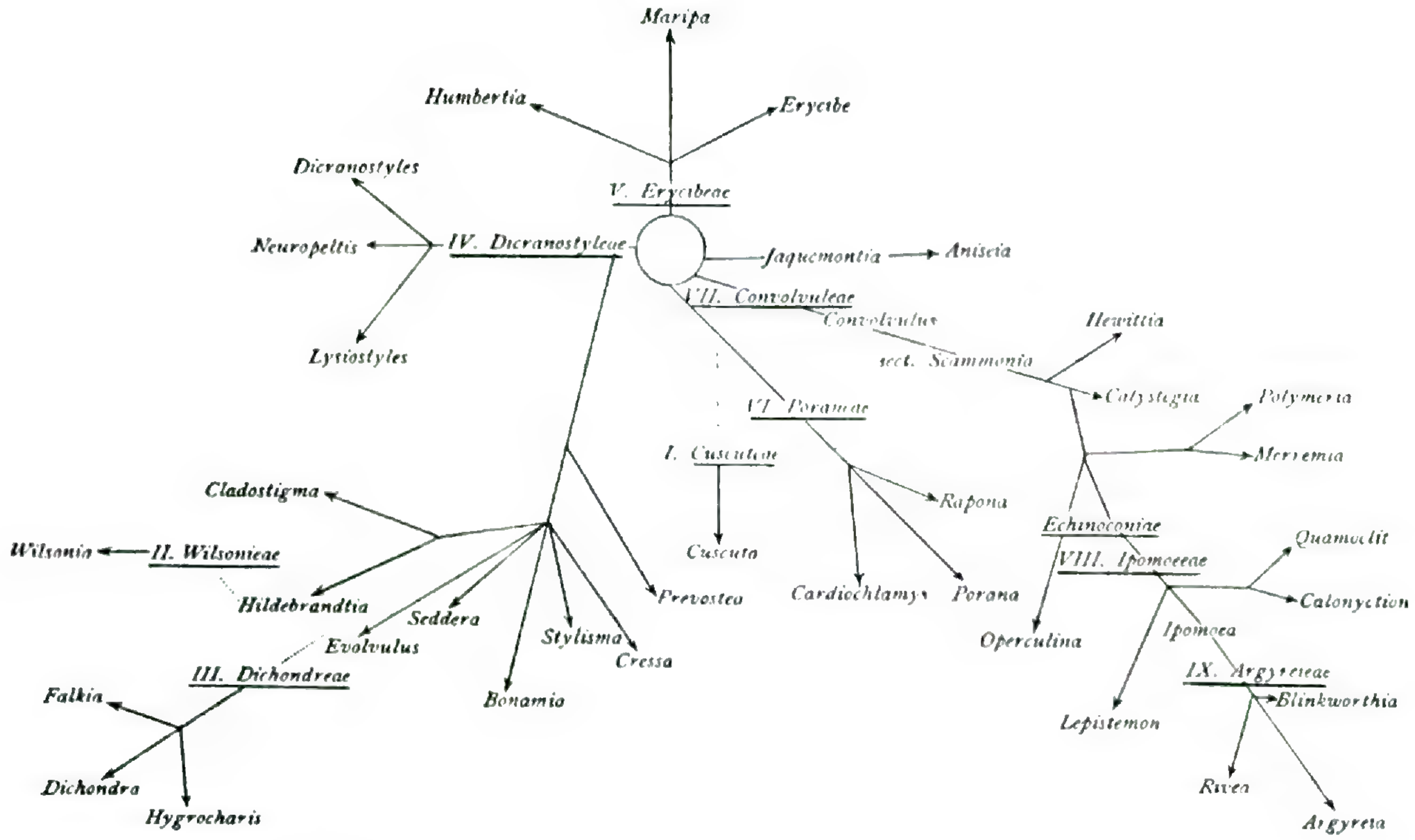


FIGURE 32. Hallier's (1893) phylogenetic scheme for the Convolvulaceae.

6. DICHONDREAE (Choisy) Choisy *in* DC. Prodr. 9: 325. 1845.

Dichondraceae Dumortier, Anal. Fam. 20, 24. 1829.
?Wilsonieae Hall. f., Bot. Jahrb. Syst. 16: 568. 1893.
Dichondroideae Roberty, Candollea 14: 22. 1952.
Wilsonioideae Roberty, Candollea 14: 23. 1952.
Nephrophylleae Roberty, Candollea 14: 28. 1952.
Wilsoniinae (Hall. f.) v. Ooststr., Fl. Males. 4: 389. 1953.
Dichondrinae (Choisy) v. Ooststr., Fl. Males. 4: 389. 1953.

Genera included: *Dichondra* Forst., 1776; *Falkia* L. f., 1781; ?*Wilsonia* R. Br., 1810; *Nephrophyllum* A. Rich., 1850.

Only two phylogenetic schemes have been published for the Convolvulaceae (Hallier, 1893; Roberty, 1964). Of these Hallier's is the most natural, but it contains parts which must be changed in view of new data.

If one can judge from Hallier's illustration of familial relations (Fig. 32), it is clear that he considered the Erycibeae, Convolvuleae, Dicranostyleae, and Poraneae as primitive tribes. The Convolvuleae and Dicranostyleae contain specialized members, but they form a basic part of the family. This interpretation has not been greatly changed by new evidence, but more specific points within the relationships proposed by Hallier must be adjusted.

The closest allies of the Erycibeae seem to lie within the Convolvuleae *sensu restricto* (Fig. 33). The campanulate corollas of *Maripa* subg. *Ripama* and the modified linear stigmas of *Dicranostyles* subg. *Kuhlmanniella* suggest close relations between the Erycibeae and the Convolvuleae, since these characters are not found elsewhere in the family. The often elliptical leaves and the general aspect of these groups also suggest this affinity. Cytologically the Convolvuleae, as I have restricted it, forms a line distinct from the remainder of the family; the

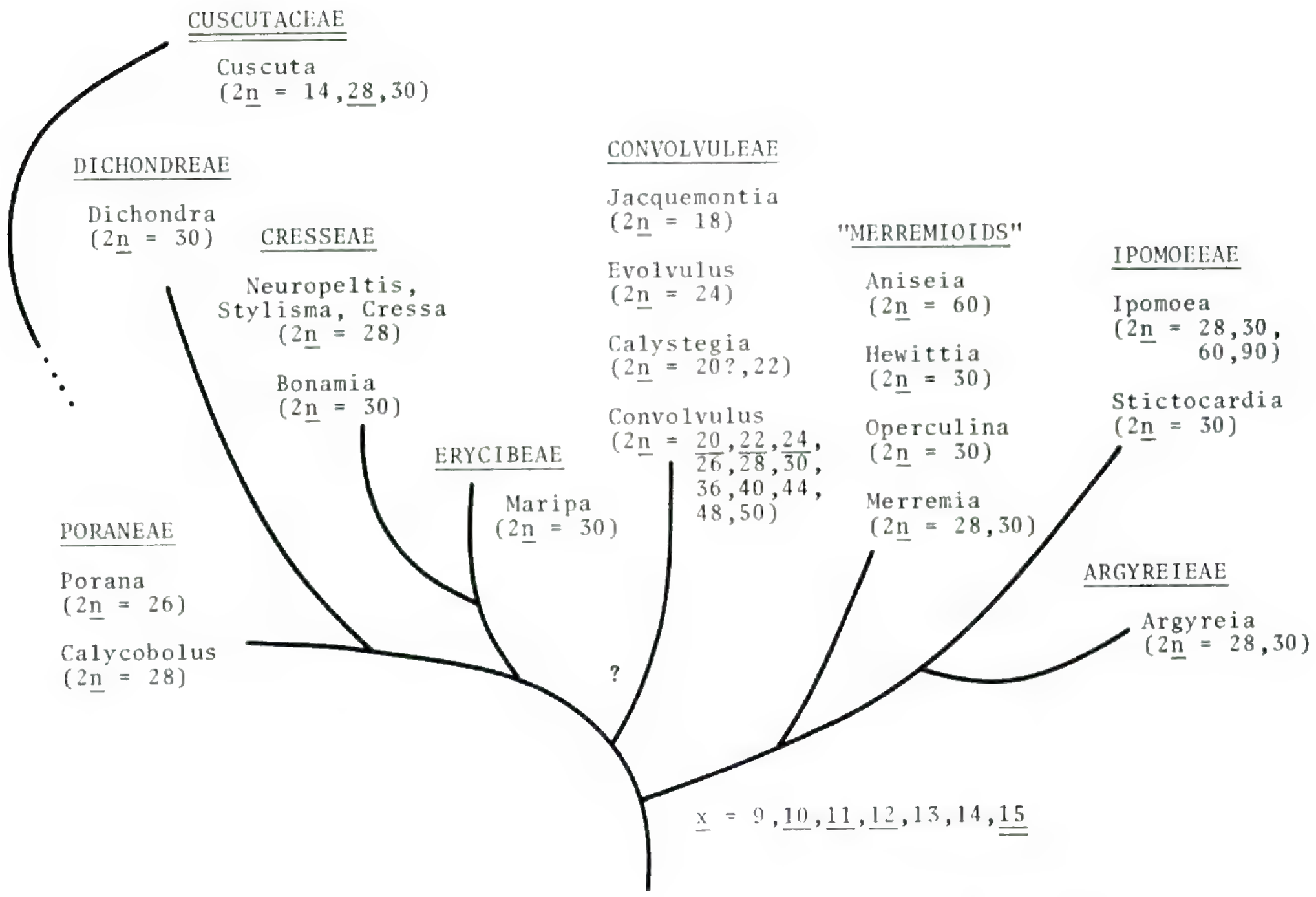


FIGURE 33. A proposed new phylogenetic scheme for the Convolvulaceae.

Convolvuleae is based on $n = 10$, 11, and 12, while the remainder of the family is based chiefly on $n = 15$. This cytological coherence of the Convolvuleae does not necessarily deny their relations with the Erycibeae which, as far as is known, are based on $n = 15$.

Relations between the Erycibeae and the Cresseae (= Dicranostyleae *sensu* Hallier) are clear from Hallier's scheme, with *Neuropeltis* being similar in many morphological characters to *Dicranostyles* and *Lysiostyles*. The valvate aestivation of these three genera is apparently unique within the family, although the genera belong to two different tribes. These two tribes are further linked by *Bonamia* sect. *Trichantha*, which shares a non-ligneous testa with the Erycibeae. The remaining Cresseae share a ligneous testa with the Convolvuleae, the "Merremioids," and the Echinoconiae. The Erycibeae and Cresseae are also linked by the bifid stylar structure, which caused Meisner (1869) and others, to place *Dicranostyles* and *Lysiostyles* with the genera in the Cresseae *sensu* Austin to form the Dicranostyleae. The bifid styles provide a uniting character for the Erycibeae, Convolvuleae, Cresseae, Poraneae, and the Dichondreae.

The Poraneae are more distantly related to the Erycibeae, Convolvuleae, and Cresseae. This tribe, with its indehiscent fruits, liana habit, mostly elliptical leaves, and bifid styles, is clearly more similar to these three tribes than to the "Merremioids" or the Echinoconiae. While the relations between the Poraneae and the Erycibeae are somewhat distant, the relations between the Poraneae, the Dichondreae and the Cuscutaceae are much closer. As described earlier, the embryo and fruit structure of these groups is quite similar. The Dichondreae

TABLE 7. Specialization index.

1. Corolla shape
   campanulate—0
   funnelform—1
2. Corolla lobes
   deep—0
   shallow—1
3. Stamens
   exserted—0
   included—1
4. Inflorescences
   phyllothyrsiform—0
   aphyllothyrsiform—1
   mixed—1.5
   racemose to solitary—2
5. Pollen
   3-colpate—0
   pantocolpate—1
6. Pubescence
   dibrachiate balanced—0
   dibrachiate unbalanced—1
   stellate—2
7. Fruit
   1–4 seeded—0
   1 seeded—1
8. Ovary
   globose—0
   ovoid—1
   cylindric—2
9. Pollen surface
   primitive—0
   advanced—1
10. Styles
    free—0
    ± half fused—1
    completely fused—2
11. Anthers
    basifixed—0
    versatile—1
    neither—2
12. Cotyledons
    foliaceous—0
    mixed—0.5
    thickened—1

are clearly related to the Poraneae and not the Cresseae (= Dicranostyleae) as suggested by Hallier.

According to Hallier's scheme, the Convolvuleae form a bridge between the Erycibeae and the Ipomoeeae. I see no reason to agree with this. Hallier considered the smooth pantoporate pollen of *Calystegia* an intermediate stage between the colpate pollen typical of the Erycibeae and Convolvuleae and the pantoporate, spinose pollen of the Echinoconiae. The smooth pantoporate of *Calystegia* and spiny pantoporate pollen of the Echinoconiae are more likely derived through parallel evolution from simpler forms than through one giving rise to the other. As a result of this interpretation of the pollen and the data presented above, I have derived the Ipomoeeae and the Argyreieae from a line separate from that which gave rise to the Convolvuleae and Erycibeae. Because of the corolla shape, leaf shape and chromosome numbers based on $n = 14$ and 15, I am deriving the "Merremioids" from a similar ancestor with the Ipomoeeae and Argyreieae.

2. GENERIC RELATIONS

Although a natural assemblage of taxa, the Convolvulaceae are nevertheless extremely difficult to delimit generically. Its genera have long been subject to different interpretations (*e.g.* Linnaeus, 1764; R. Brown, 1810; Choisy, 1845; Gray, 1862; Bentham & Hooker, 1873; Hallier, 1893; Peter, 1891; Small, 1933; O'Donell, 1941, 1953, 1959*b*, 1960*a*; Barroso, 1945, 1947; Fernald, 1950; Knight, 1958; Wilson, 1960; Shinners, 1962; Lewis & Oliver, 1965; Myint, 1966; Myint & Ward, 1968; Long, 1969). Genera are often separated by what appear to be trivial characters, at least to workers who have not studied the family closely. They tend to reject interpretations (and often data) of those who have studied the family intensively. Yet subtle and difficult characters are often just as indicative of natural grouping as are the more obvious ones.

The three American genera *Maripa*, *Dicranostyles*, and *Lysiostyles*, and the Old World genera *Humbertia* and *Erycibe* form a natural group within the family. These five genera were surely derived from a common ancestory.

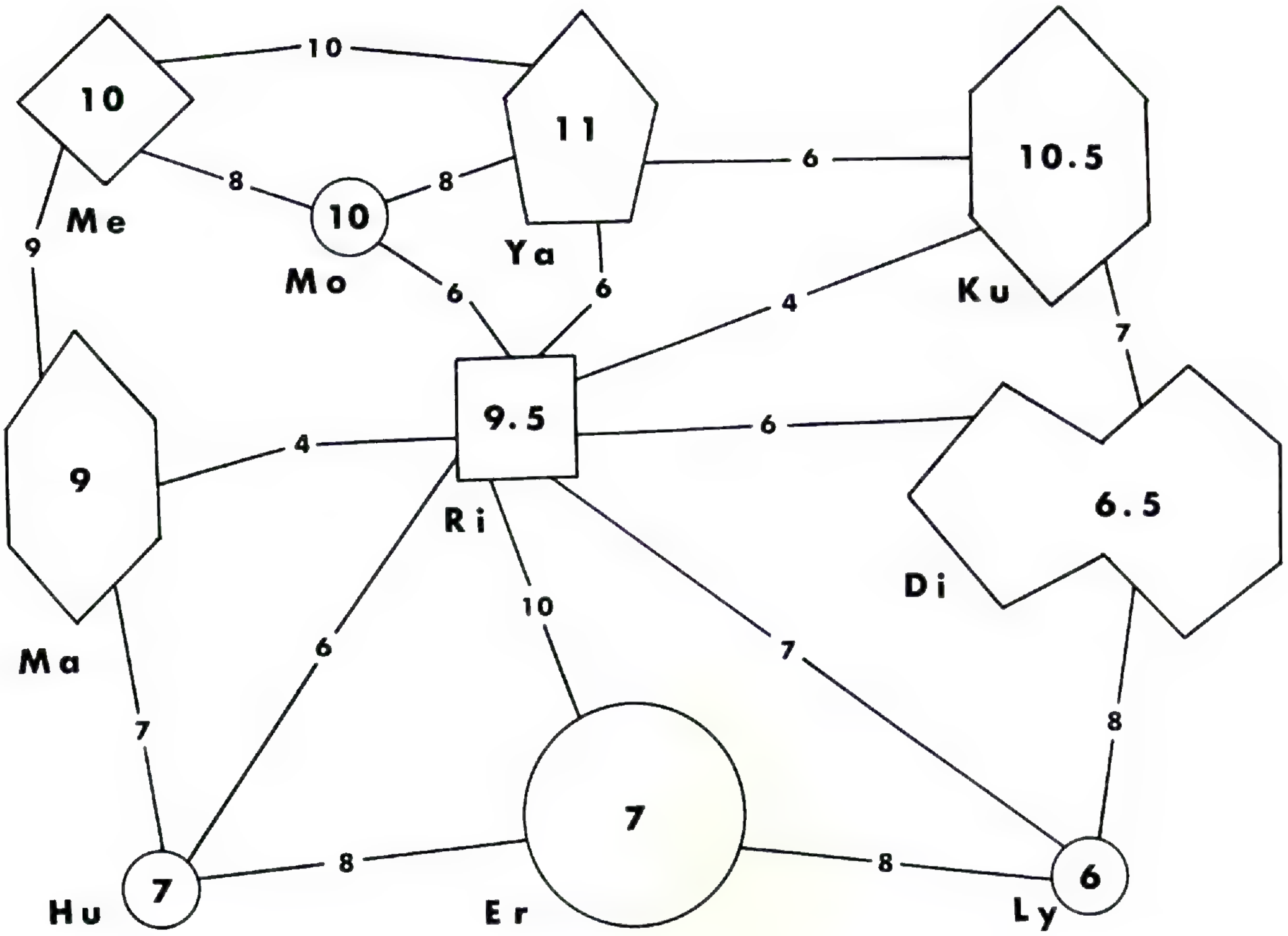


FIGURE 34. Diagrammatic scheme illustrating the reticulate character distribution in the Erycibeae. Numbers inside geometric designs indicate the total specialization value of the species in that taxon. The smaller numbers connecting the lines designate the total number of characters from the specialization index list shared by the groups. Abbreviation of names: Di = *Dicranostyles* subg. *Dicranostyles*. Er = *Erycibe*. Hu = *Humbertia*. Ku = *Dicranostyles* subg. *Kuhlmanniella*. Ly = *Lysiostyles*. Ma = *Maripa* sect. *Maripa*. Me = *Maripa* subsect. *Melofructae*. Mo = *Maripa* subsect. *Mouroucoa*. Ri = *Maripa* subg. *Ripama*. Ya = *Maripa* subsect. *Yacuascae*.

Yet each group of species has different combinations of morphological structures which are distinctive. These structures vary, and a specialization index (Table 7) may be effectively applied to determine the relative evolutionary advancement of each group (Fig. 34). The values given for each character are based on phylogenetic interpretations of similar structures in other groups (Davis & Heywood, 1963; Myint, 1966).

When this index is applied, the taxa may be grouped in order of increasing specialization:

> 6, *Lysiostyles*; 6.5, *Dicranostyles* subg. *Dicranostyles*; 7, *Humbertia*; 7, *Erycibe*; 9, *Maripa* sect. *Maripa*; 9.5, *Maripa* subg. *Ripama*; 10, *Maripa* subsect. *Mouroucoa*; 10, *Maripa* subsect. *Melofructae*; 10.5, *Dicranostyles* subg. *Kuhlmanniella*; 11, *Maripa* subsect. *Yacuascae*.

When an index with a relatively small number of characters is applied to such a large group, the results are clearly not perfect. Nevertheless, the trends indicated by this method are useful in understanding the phylogeny of the taxa involved.

TABLE 8. Historical development of a tribal classification of the Convolvulaceae.

CHOISY (1833)
Sectio I. Argyreieae
(*Humbertia, Maripa*)
Sectio II. Convolvuleae
Sectio III. Dichondreae
Sectio IV. Cuscuteae
Genera et Ordine Rejecta
Erycibe . . . . . Boragineae

ENDLICHER (1841)
Subordo I. Dichondreae
Subordo II. Convolvuleae
(*Humbertia, Maripa*)
Convolvulaceis affinis;
Erycibeae, Cuscuteae

CHOISY (1845)
Tribus I. Argyreieae
(*Humbertia, Maripa*)
Tribus II. Convolvuleae
Tribus III. Dichondreae
Tribus IV. Cuscuteae

LINDLEY (1853)
1. Convolvuleae
(*Maripa, Humbertia, Dicranostyles, Lysiostyles*)
2. Dichondreae
Additional genera—
Erycibe
Cuscutaceae

MEISNER (1969)
Tribus I. Convolvulinae
Subtribus 1. Argyreieae
(*Maripa*)
Subtribus 2. Convolvuleae
Subtribus 3. Dicranostyleae
(*Dicranostyles, Lysiostyles*)
Tribus II. Dichondreae

BENTHAM & HOOKER (1873)
Tribus I. Convolvuleae
(*Erycibe, Humbertia, Maripa, Lysiostyles, Dicranostyles*)
Tribus II. Dichondreae
Tribus III. Nolaneae
Tribus IV. Cresseae
Tribus V. Cuscuteae

BAILLON (1891)
Série I. Convolvuleae
(*Dicranostyles, Lysiostyles, Erycibe, Maripa*)
Série II. Cresseae
Série III. Cuscuteae
Série IV. Dichondreae

PETER (1891)
Subfam. I. Convolvuloideae
Tribus 1. Dichondreae
Tribus 2. Dicranostyleae
(*Dicranostyles, Lysiostyles*)
Tribus 3. Hildebrandtieae
Tribus 4. Convolvuleae
Subtrib. a. Argyreiinae
(*Maripa, Humbertia*)
Subtrib. b. Convolvulinae
Tribus 5. Erycibeae
(*Erycibe*)
Subfam. II. Cuscutoideae

HALLIER (1893)
"Subfam." I. Psiloconiae
Tribus 1. Cuscuteae
Tribus 2. Wilsonieae
Tribus 3. Dichondreae
Tribus 4. Dicranostyleae
(*Dicranostyles, Lysiostyles*)
Tribus 5. Poraneae
Tribus 6. Erycibeae
(*Erycibe, Maripa, Humbertia*)
Tribus 7. Convolvuleae
"Subfam." II. Echinoconiae
Tribus 8. Ipomoeeae
Tribus 9. Argyreieae

If the same criteria from the specialization index are used to compute the total number of characters shared by the taxa, an interesting reticulate pattern of characters emerges. This pattern, unlike the situation in some other plant groups (Ownbey, 1950; Wagner, 1954; Smith & Levin, 1963), has apparently not been produced by hybridization, but probably by parallel evolution.

Taxa that share characteristics probably are phylogenetically similar, the more characters the more closely allied. An examination of Fig. 34, for example, will show that the subgeneric taxa of *Maripa* subg. *Maripa* are connected by 8 to

TABLE 8. Continued.

ROBERTY (1952)
Subfam. 1. Humbertoideae
Subfam. 2. Dichondroideae
Subfam. 3. Wilsonioideae
Subfam. 4. Hildebrandtioideae
Subfam. 5. Eryciboideae
Subfam. 6. Poranoideae
Tribe I. Neuropeltideae
Tribe II. Dipteropeltideae
Tribe III. Prevosteae
Tribe IV. Poraneae
Tribe V. Lepistemonopseae
Subfam. 7. Convolvuloideae
Tribe I. Evolvuleae
Tribe II. Nephrophylleae
Tribe III. Cresseae
Tribe IV. Convolvuleae
Tribe V. Ipomoeeae
Subfam. 8. Argyreioideae
Tribe I. Lysiostyleae
Tribe II. Dicranostyleae
Tribe III. Argyreieae
Tribe IV. Blinkworthieae

OOSTSTROOM (1953)
Subfam. A. Cuscutoideae
Tribe I. Cuscuteae
Subtr. Cuscutinae
Subfam. B. Convolvuloideae
Tribe II. Convolvuleae
Subtr. Wilsoniinae
Subtr. Dichondrinae
Subtr. Dicranostylinae
(*Evolvulus, Bonamia, Neuropeltis*)
Subtr. Poraninae
Subtr. Erycibinae
Subtr. Convolvulinae
Tribe III. Ipomoeeae
Subtr. Ipomoeinae
Subtr. Argyreiinae

MELCHOIR (1964)
Subfam. I. Humbertioideae
Subfam. II. Dichondreae
Subfam. III. Convolvuloideae
Tribe 1. Wilsonieae
Tribe 2. Hildebrandtieae
Tribe 3. Erycibeae
Tribe 4. Poraneae
Tribe 5. Convolvuleae
(incl. Ipomoeeae)
Tribe 6. Argyreieae
(*Dicranostyles*)
Subfam. IV. Cuscutoideae

ROBERTY (1964)
Subfam. I. Argyreioideae
Tribe 1. Blinkworthieae
Tribe 2. Argyreieae
Tribe 3. Dicranostyleae
Tribe 4. Lysiostyleae
Tribe 5. Erycibeae
Subfam. II. Convolvuloideae
Tribe 6. Ipomoeeae
Tribe 7. Convolvuleae
Tribe 8. Cresseae
Tribe 9. Nephrophylleae
Tribe 10. Evolvuleae
Subfam. III. Poranoideae
Tribe 11. Lepistemonopsideae
Tribe 12. Poraneae
Tribe 13. Prevosteae
Tribe 14. Hildebrandtieae
Tribe 15. Neuropeltideae

HAGNAUER (1964)
Subfam. I. Cuscutoideae
Subfam. II. Convolvuloideae
Tribe 1. Dichondreae
Tribe 2. Dicranostyleae
(*Dicranostyles, Lysiostyles*)
Tribe 3. Convolvuleae
Tribe 4. Poraneae
Tribe 5. Erycibeae
(*Erycibe*)
Tribe 6. Ipomoeeae
Tribe 7. Argyreieae
(*Humbertia, Maripa*)

SHAW (1966)
Tribe 1. Dichondreae
Tribe 2. Dicranostyleae
(*Dicranostyles*)
Tribe 3. Hildebrandtieae
Tribe 4. Convolvuleae
Tribe 5. Poraneae
Tribe 6. Ipomoeeae
Tribe 7. Argyreieae
Tribe 8. Erycibeae
(*Erycibe*)

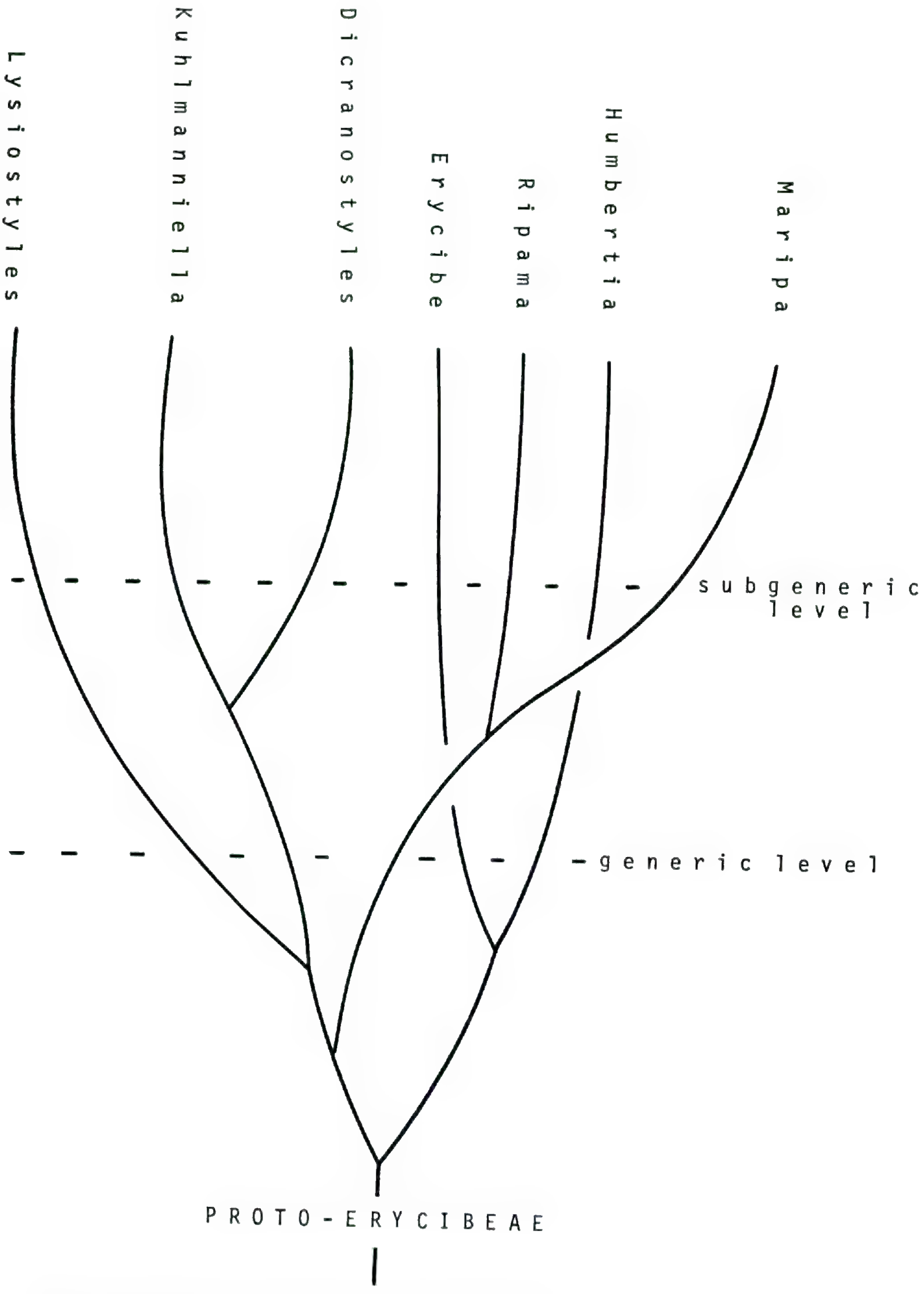


FIGURE 35. Probable phylogeny for the tribe Erycibeae.

10 shared characters, while the most they share with subg. *Ripama* is 6 characters. Within subg. *Maripa* the subsect. *Melofructae* and *Yacuascae* share 10 characters, indicating a close relation between them. However, these subsections share fewer characters with other members of the genus.

At the same time the subg. *Ripama* has in common with the genus *Erycibe* a total of 10 characters. If plants of subg. *Ripama* and *Erycibe* grew on the same continents, botanists would undoubtedly have described them as two different related genera. I have chosen not to recognize subg. *Ripama* as a distinct genus, however, because of the close similarity of its species with the others of *Maripa*.

Applying the relations suggested in Fig. 34 with other morphological and anatomical data it is possible to prepare a dendroid phylogeny for the tribe (Fig. 35). The first major division of the phylogeny divides the genera between the Old and New Worlds. This division partially reflects their antiquity and long isolation.

3. Taxonomy

A. HISTORICAL BIBLIOGRAPHY

Around the beginning of the twentieth century it was customary for botanists to provide a bibliography in condensed form at the beginning of systematic works. This practice is currently denounced as unnecessary and space consuming. It is admittedly space consuming, but in a work of monographic nature a list of all publications dealing with the groups involved may be potentially valuable and time saving to future workers. For these reasons I have compiled the following bibliography. Works containing species descriptions only are not included.

Maripa Aublet, Hist. Pl. Gui. Fr. 1: 230, *t. 91*. 1775.

Dicranostyles Benth., London Jour. Bot. 5: 355. 1846.

Lysiostyles Benth., London Jour. Bot. 5: 355. 1846.

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B. TRIBAL DESCRIPTION

ERYCIBEAE (Endl.) Hall. f., Bot. Jahrb. Syst. 16: 576. 1893.

Erycibeae Endl., Enchir. Bot. 322. 1841, as "Convolvulaceis affines *Erycibeae."
Maripeae Webb & Berth., Nat. Hist. Can. Isl. 3. 2(3): 27. 1844.
Dicranostyleae Meisn. *in* Mart., Fl. Bras. 7: 205. 1869, pro parte minore.
Convolvuloideae-Dicranostyleae Peter *in* Engler & Prantl, Nat. Pflanzenfam. 4(3a): 14–18. 1893, pro parte minore.
Convolvuloideae-Convolvuleae-Argyreiinae Peter *in* Engler & Prantl, Nat. Pflanzenfam. 4(3a): 20–22. 1893, pro parte minore.
Convolvuloideae-Erycibeae Peter *in* Engler & Prantl, Nat. Pflanzenfam. 4(3a): 36–37. 1893.
Erycibinae (Endl.) v. Ooststr. *in* v. Steenis, Fl. Males. 4: 389. 1953.
Dicranostylinae (Meisn.) v. Ooststr. *in* v. Steenis, Fl. Males. 4: 389. 1953, pro parte minore.

Lianas, scandent shrubs, or rarely trees. *Leaves* alternate to subopposite, simple, elliptic to ovate or obovate, the base acute, obtuse or rarely subcordate, the apex acute, acuminate, obtuse, or emarginate, mostly coriaceous; indument mostly dibrachiate or stellate. *Inflorescences* terminal on lateral branches or axillary, paniculate-thyrsiform, racemose, or rarely solitary. *Flowers* pentamerous; sepals quincuncial, equal to subequal, mostly coriaceous to subcoriaceous; corolla funnelform, cylindric-funnelform, campanulate-funnelform, or campanulate; stamens either included or excluded, if excluded either regular or irregular, the anthers longitudinally introrse; disc present or absent, if present often with five lobes; ovary rotund, cylindric to conic, with an incomplete septum in lower portion, the style entire, bifid or absent. *Fruits* nut-like or baccate, 1–4 seeded through abortion; seeds glabrous, surrounded by a gelatinous, often sweet and fragrant perisperm, the testa soft, coriaceous to chartaceous, the embryo erect and straight or slightly folded, or with the radicle bent against the corrugate cotyledons.

Leaf structure bifacial; spongenchyma often with large cavities and branched cells; stomata usually with two accessory cells, absent from the upper surface; trichomes 2–many-branched, glanular trichomes with horizontal and vertical walls, not chambered, margins usually sinuate on head; fibrovascular bundles protected either below or on both surfaces by a sclerenchyma layer; glandular cells solitary, sparce in the phloem or mesophyll, rarely in the cotyledons.

Pollen 3-colpate, pantopolycolpate, or 3-colporate? (in *Humbertia*).

Old World genera: *Humbertia* (Madagascar) and *Erycibe* (Indo-Malaysia and Australia).

New World genera: *Maripa* (Belize to Bolivia), *Dicranostyles* (northern South America), and *Lysiostyles* (Guianas).

Key to Genera of Erycibeae

a. Leaves spathulate; flowers solitary, ovules numerous; trees in Madagascar ..... (*Humbertia*)
aa. Leaves elliptical, ovate, obovate to oblong; flowers in compound-panicles or racemes, ovules 4; shrubs and vines widely distributed.
  b. Style absent and stigma sessile; corolla lobes bifid ..... (*Erycibe*)
  bb. Style elongate, short in some species of *Dicranostyles*, but stigma never sessile; lobes entire.
    c. Flowers 2–10 mm long; anthers either versatile or with an enlarged flattened, elongate connective; fruiting sepals 1–3.5 mm long.
      d. Anthers versatile, connective inconspicuous; corolla lobes acute to obtuse at apex ..... 2. *Dicranostyles*
      dd. Anthers not versatile, but with an enlarged, flattened, elongate connective extending 1.5–2 times the length of the basifixed thecae; corolla lobes extending into a long attenuate, almost filiform apex ..... 3. *Lysiostyles*
    cc. Flowers (10–)14–60 mm long; anthers dorsi-fixed and not versatile, the connective small; fruiting sepals 4–16 mm long ..... 1. *Maripa*

1. Maripa

Maripa Aublet, Hist. Pl. Gui. Fr. 1: 230, *tab. 91.* 1775.

Mouroucoa Aublet, Hist. Pl. Gui. Fr. 1: 142, *tab. 54.* 1775.
Maireria Scopoli, Int. Hist. Nat. 192. 1777.
Ehretia Lam., Encyl. Méth. Bot. 1: 527. 1783, *non* L., Syst. Veg., ed. 10. 936. 1759.
Murucoa Gmelin *in* L., Reg. Veg. 1: 344. 1796.
Murueva Raf., Ann. Gén. Sci. Phys. 8: 270. 1821.
Gaseranthus Poit. *ex* Meisn. *in* Mart., Fl. Bras. 7: 206. 1869.

Lianas reaching over 30 m; larger stems fluted, to 30 cm in diameter, younger stems often angled; pith ±round in cross-section, light brown. *Leaves* alternate to subopposite, simple, mostly elliptical, ovate or obovate to oblong; petioles canaliculate; exstipulate; venation brochidrodromus; glabrous to glabrescent or occassionally stellate. *Inflorescences* terminal on lateral branches or axillary, paniculate-thyrsiform or racemose; branches usually pubescent with dibrachiate or stellate indument and/or peltate glandular scales; bracts triangular to obovate, persistent to caducous, glabrous or pubescent, the bracteoles squamiform, glabrous or pubescent. *Flowers* pentamerous, often fragrant; sepals quincuncial, ovate, oblong, broadly ovate to rotund, the innner often emarginate, the outer acute to rounded, equal to subequal in length, the inner usually wider than long, mostly coriaceous with membranaceous margins, ciliate, the pubescence appressed dibrachiate, stellate or peltate; corolla funnelform, campanulate-funnelform, cylindric-funnelform or campanulate, white to violet or pinkish, medium-small (10 mm) to large (60 mm), the lobes shallow, occasionally deep, mostly rounded, occasionally acute, occasionally undulate, appressed pubescent on interplicae, glabrous on plicae; stamens epipetalous, mostly included, the filaments filiform above with the base triangular-dilate and glandular shaggy, the anthers dorsifixed, sub-sagittate to sagittate, narrowly ovate, longitudinally introrse; disc cupuliform, often with five lobes, the lobes probably nectiferous;

ovary rotund, cylindric to conic, incompletely bilocular with a partial septum in lower portion, mostly glabrous, the apex occasionally pubescent, the style entire, rarely divided for ½–⅓ length or less, mostly glabrous, occasionally pubescent at apex, the stigma capitate, lobes two, closely appressed if style entire, or free, one lobe often slightly below the other. *Fruits* nut-like, rounded to ellipsoid, the pericarp ligneous, firm to hard, 1–4 seeded through abortion; seeds glabrous, ovoid to oblong-ellipsoid, rounded, flattened or trigonous if more than one per fruit, surrounded by a gelatinous, often sweet and fragrant perisperm, the testa soft, chartaceous to coriaceous, the embryo erect, latiplicate, rarely lati-longiplicate, the endosperm scanty or absent, cartilaginous, the cotyledons thick, rarely thin, incumbent, the base cordate, investing, the apex rounded to slightly emarginate.

Type: *Maripa scandens* Aublet.

Pollen 3(–4–5)-colpate or pantocolpate in 4 × 4 × 4, 4 × 4, or less commonly 5 × 5 × 5, 5 × 5, 3 × 3 ×3, or 3 × 3 patterns within the same flower, oblate to spheroidal; chromosomes known for *M. reticulata* only, $2n = 30$; flowering peaks in January to April and October to November; seeds used as food by monkeys (the genus *Cebus*, Cebidae), some birds, particularly parrots, and man.

SYNOPSIS OF INFRAGENERIC TAXA

a. Corolla campanulate, styles and stamens exserted, inflorescences racemose or rarely aphyllothyrsiform, ovary globose or cylindric, flowering peak January–March, pollen mostly 12 pantocolpate ..... subgenus 1. *Ripama*

Including: 1. *M. elongata* Ducke; 2. *M. reticulata* Ducke; 2b. *M. reticulata* var. *rugosa* (Ducke) D. Austin; 3. *M. longifolia* Sagot *ex* Hall. f.; 4. *M. axilliflora* Mart. *ex* Meisn.

aa. Corolla funnelform, campanulate-funnelform, or cylindric-funnelform, styles and stamens included, inflorescences phyllothyrsiform or aphyllothyrsiform, ovary cylindric, acute-cylindric or conic to conic-ovoid, flowering March–April and October–November, pollen 3-zonocolpate, 6-pantocolpate, 8-pantocolpate or 12-pantocolpate ..... subgenus 2. *Maripa*

b. Corolla 10–25 mm long and 10–12(–20) mm wide when fully open.

c. Inflorescences phyllothyrsiform, stellate trichomes absent, flowering peak October–November, fruits with 1(–2) seeds ..... sect. *Maripa*

Including: 5. *M. scandens* Aublet; 6. *M. densiflora* Benth.; 7. *M. janusiana* D. Austin; 8. *M. paniculata* Barb.-Rodr.; 9. *M. glabra* Choisy; 10. *M. williamsii* v. Ooststr.

cc. Inflorescences aphyllothyrsiform, stellate trichomes present on inflorescence branches, flowering peak March–April, fruits with 1–4 seeds ..... subsect. *Yacuascae*

Including: 16. *M. repens* Rusby; 17. *M. fasciculata* v. Ooststr.; 18. *M. pauciflora* D. Austin; 19. *M. putumayana* D. Austin.

bb. Corolla 25–60 mm long and 15–40 mm wide when fully open.

d. Outer sepals glabrous, fruits with 1–4 seeds, flowering peak March–April, pollen pantocolpate.

e. Sepals 10–16 mm long, corolla 35–60 mm long, inflorescences aphyllothyrsiform ..... subsect. *Mouroucoa*

Including: 11. *M. violacea* (Aublet) v. Ooststr. *ex* Lanjouw & Uittien.

ee. Sepals 6–8 mm long, corolla 25–40 mm long, inflorescences phyllothyrsiform ..... subsect. *Melofructae*

Including: 12. *M. nicaraquensis* Hemsley; 13. *M. peruviana* v. Ooststr.; 14. *M. panamensis* Hemsley; 15. *M. stellulata* Steyermark.

dd. Outer sepals pubescent, fruits with 1(–2) seeds, flowering peak October–November, pollen 3-zonocolpate ..... sect. *Maripa*

Including: 5 *M. scandens* Aublet

Artificial Key to Species

a. Inflorescences in axillary racemes.
  b. Secondary veins average less than 10 pairs per leaf, leaves with some dibrachiate trichomes below; fruits with sepals reflexed ..... 2. *M. reticulata*
  bb. Secondary veins average more than 10 pairs per leaf, leaves glabrous or with peltate trichomes below; fruits with sepals appressed.
    c. Fruits smooth, shiny, infructescence branches sparsely covered with peltate scales ..... 4. *M. axilliflora*
    cc. Fruits striate, dull, infructescence glabrous ..... 3. *M. longifolia*

aa. Inflorescences fasciculate-cymose, sub-racemose, sub-umbelliform, or paniculate-thyrsiform.
  d. Inflorescences without leaves among lower inflorescence branches (aphyllothyrsiform).
    e. Inflorescences mostly less than 8 cm long.
      f. Bracts caducous in bud, corolla broad campanulate-funnelform ..... 19. *M. putumayana*
      ff. Bracts persistent to fruits, corolla funnelform.
        g. Ovary with a short villose apex ..... 16. *M. repens*
        gg. Ovary glabrous.
          i. Leaves chartaceous, secondaries not deeply impressed above nor prominent below, filaments inserted 5 mm above corolla base ..... 17. *M. fasciculata*
          ii. Leaves coriaceous, secondaries deeply impressed above and very prominent below, filaments inserted 3 mm above corolla base ..... 18. *M. pauciflora*
    ee. Inflorescences elongate, cylindrical thyrses 8–30 cm long.
      j. Inflorescence branches densely covered with yellow stellate indument, bracts stellate pubescent, corolla campanulate, ovary glabrous ..... 1. *M. elongata*
      jj. Inflorescence branches with peltate indument, bracts with glandular peltate indument, corolla funnelform, ovary with a short-villose apex ..... 16. *M. repens*
  dd. Inflorescences with leaves among the lower to middle branches (phyllothyrsiform).
    k. Lower side of leaves and branches of inflorescence densely furfuraceo-stellate ..... 15. *M. stellulata*
    kk. Lower side of leaves and branches of inflorescence with appressed dibrachiate trichomes and/or peltate scales of various forms.
      l. External sepals appressed pubescent outside.
        m. Sepals light in color (whitish or yellowish) because of dense cover of hairs ..... 5. *M. scandens*
        mm. Sepals dark in color (purplish with only traces of white hairs), yellow-white hairs appearing only with magnification ..... 8. *M. paniculata*
      11. External sepals glabrous or with peltate scales outside.
        n. Internal sepals appressed dibrachiate pubescent outside.
          o. Corolla ca. 20 mm long, ovary ca. 2 mm long, sepals appressed in fruits.
            p. Leaves with sunken oil glands above (visible only with more than 10× magnification), glabrous below, ovary glabrous ..... 9. *M. glabra*
            pp. Leaves without oil glands but with dense cover of whitish peltate scales above and below, ovary glabrous or pubescent.
              q. Sepals ± same length, appressed in bud, ovary glabrous, corolla indument dibrachiate and medifixed ..... 7. *M. janusiana*
              qq. Sepals unequal, outer 2 shorter, spreading in bud, ovary apex usually villose, corolla indument dibrachiate and attached at end of terminal cell ..... 6. *M. densiflora*

oo. Corolla 25–60 mm long, ovary 4–6 mm long, sepals reflexed in fruits.
r. Corolla 35–60 mm long and 30–40 mm wide, calices at least 10 mm long and 10 mm wide ..... 11. *M. violacea*
rr. Corolla 25–35 mm long and 10–25 mm wide, calices smaller than 10 mm long and wide.
s. Leaves thick coriaceous, rugose below, veins not prominent below, fruits striate ..... 14. *M. panamensis*
ss. Leaves chartaceous to subcoriaceous, reticulate below, veins prominent below, fruit smooth to slightly striate ..... 12. *M. nicaraguensis*

nn. Internal sepals glabrous outside.
t. Sepals appressed to base of fruit, bracts persistent to fruiting ..... 13. *M. peruviana*
tt. Sepals reflexed from fruit base, bracts mostly caducous in flower.
u. Fruits less than 20 mm long, shiny, non-apiculate, flowers ca. 20 mm long ..... 10. *M. williamsii*
uu. Fruits more than 20 mm long, dull, apiculate, flowers 25–35 mm long.
v. Leaves thick coriaceous, rugose below, veins not prominent below, fruit striate ..... 14. *M. panamensis*
vv. Leaves chartaceous to subcoriaceous, reticulate below, veins prominent below, fruit smooth to slightly striate ..... 12. *M. nicaraguensis*

Subg. 1. **Ripama** D. Austin, subg. nov.

Corollis campanulatis saepe profunde lobatis, genitaliis exsertis, inflorescentiis racemosis vel aphyllothyrsiformis, anthesi praecipue a Januariis ad Martiis, irregulariter mensibus aliis, ovariis globosis vel cylindricis. (Typus *Maripa elongata* Ducke.)

1. **Maripa elongata** Ducke, Arq. Inst. Biol. Veg. 4: 60. 1938.

Lianas; stems terete, slightly angled, brown, the bark with white striae. *Leaves* with petioles (15–)20–25(–30) mm long; blades elliptic to ovate, rarely oblanceolate, 11.5–18(–30) cm long, 4.5–10(–13) cm wide, the base obtuse, the apex shortly acuminate, coriaceous, the secondaries 10–11(–13) pairs; sparsely appressed pubescent above, scattered stellate below. *Inflorescences* axillary, cylindric-thyrsiform, 10–20(–30) cm long, commonly 3.5–4.5 cm in diameter, the rachis and branches densely yellowish stellate pubescent; bracts triangular, ovate or lanceolate, acute, 1.5–7 mm long, stellate pubescent. *Flowers* fragrant, with pedicels 2–3 mm long; sepals ovate to broadly ovate, 4–5 mm long and 4–6 mm wide, coriaceous, with membranaceous margins, ciliate, the outside glabrous except for stellate trichomes at base; corolla campanulate, white to light rose, 13–16 mm long, the lobes obtuse; stamens shortly exserted at lobes, the filaments 7 mm long, inserted 4 mm above corolla base, the anthers narrowly ovate, basally sagittate, 3.5 mm long; ovary cylindric, 2.5–3 mm long, ca. 1.5 mm in diameter, glabrous, the style 12 mm long, glabrous. *Fruits* broadly ellipsoid to obovoid, 18–20 mm long, 12–20 mm in diameter, the surface almost smooth, with slight traces of striae, dark brown, the calyx reflexed to 180° or more; seeds 1, flattened ellipsoid to obovoid, ca. 12 mm long, 9–10 mm in diameter.

Holotype: Brazil, Amazonas, Manaus, 24.3.1937, *Ducke RB 35586* RB; isotypes G, IAN, K, NY, U, US.

Rio Negro Basin of Brazil; terra firme, várzea, along riversides, high forest and old capoeiras; flowering February to June; fruiting May to October.

BRAZIL.[3] AMAZONAS: Manaus, Igarape da Cachoeira do Tarumá, terra umida, fls alvas, 19.4.1955, *Chagas 979* (IAN, INPA). Manaus, margem do Igarape do Parque 10, terra firme, arenoso, capoeirão, frts verde amarelados, trepadeira escandente com gavinhas, 25.7.1956, *Chagas INPA 3983* (INPA, RB). Manaus, Frances Novo, arenoso, umido, frts pretos, 3.10.1956, *Coelho & Chagas INPA 4214* (INPA, RB). Manaus, prope rivulum ad Estrada do Aleixo, corolla alba, 12.3.1932, *Ducke RB 24403* (K, RB, U, US). Manaus, capoeirão alim da Cachoeirinha, logar alto, fls brancas, 24.3.1932, *Ducke RB 24404* (RB). Manaus, mata dos arredores do Cachoeira do Mindu, calice verde, corola branca, estames amarelo-palido, flor com cheiro doce, 24.3.1937, *Ducke RB 35586* (G, IAN, K, NY, 3 sheets RB, U, US). Rio Negro super Santa Izabel loco Jacamim, ad ripas, fls albis, 6.3.1936, *Ducke RB 35587* (RB, US). Tapurucoara, Rio Negro, high forest, light rosy fls, 27.6.1947, *Froes 22426* (IAN, INPA). Manaus, Igarape da Cachoeira Alta do Tarumá, capoeira, fls alvas, aromaticas, 8.2.1962, *Rodrigues & Chagas 4201* (INPA, RB). Manaus, Cachoeira Alta do Tarumá, descampado, fls alvas, 20.2.1962, *Rodrigues & Chagas 4340* (INPA, RB). Manaus, Igarape da Cachoeira do Tarumá, frts maduros, 8.5.1962, *Rodrigues & Chagas INPA 12745* (INPA, RB). Middle Rio Negro, between mouth of Rio Curicuriari & Barcellos, Tapurucuara (Santa Izabel), small tree, frts green, *Schultes & Lopez 8911* (F, GH, IAN).

Fruiting specimens of this species and *Maripa reticulata* are difficult to distinguish. *Maripa elongata* apparently always has some stellate trichomes remaining on the infructescence and/or leaves, and the leaves dry yellow-green; *M. reticulata* does not have stellate indument, and the leaves dry dark brown-green. One might expect to distinguish these species by their different inflorescences, but *M. elongata* produces a racemose infructescence due to lowered fruit set.

2. **Maripa reticulata** Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 248. 1922.

Lianas or scandent shrubs; branches angular, densely pubescent when young, glabrescent. *Leaves* with petioles 10–20 mm long; blades elliptic, ovate, elliptic to obovate-oblong, 8.5–15 cm long and 3.5–12 cm wide, the base obtuse to rounded or ± cordate, the apex shortly acuminate, obtuse, rounded or retuse, thin-coriaceous, the secondaries 8–9(–11) pairs; scattered yellow-brown stellate trichomes above and below, remotely sunken glandular, glabrescent. *Inflorescences* axillary, racemose, 7–14 cm long, with some stellate pubescence when in flower, glabrescent; bracts mostly ovate, occasionally triangular, mostly caducous. *Flowers* with pedicels 10–20 mm long; sepals oblong to widely ovate or rotund, 4–5 mm long and 5–7 mm wide, subcoriaceous, glabrous or occasionally with scattered stellate trichomes; corolla campanulate, rarely campanulate-funnelform, 10–20 mm long, the lobes rotund; stamens shortly exserted between corolla lobes, the filaments 9–13 mm long, inserted 1.5–2 mm above corolla base, the anthers ovate, basally sagittate, 3–4(–5) mm long and ca. 1.5 mm wide, glabrous, the style 10–15 mm long. *Fruits* globose to shortly ellipsoid, 18–22 mm long, 14–20 mm in diameter with reticulation on surface and very faint striae, light to dark brown, shiny, the sepals reflexed to 180° or occasionally more; seeds 1–2, oblong to ellipsoid, often somewhat flattened, ca. 16–20 mm long, ca. 12–15 mm in diameter.

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[3] In the citations of specimens examined the abbreviations fl(s) and frt(s) are used for flower(s) and fruit(s) respectively.

This species is quite variable, and as Ooststroom (1932) has pointed out, certain specimens from Surinam differ somewhat from those collected in Brazil. I have considered all the collections from eastern South America as the same species. A plant collected by Ducke, and described by him as a new species, does not entirely comply with *Maripa reticulata* as represented in the eastern part of its range. This collection has been considered a western variety.

a. Leaves with scattered stellate pubescence below, mostly oblong with some obovate blades, the apex obtuse, shortly acute to retuse ..... 2a. *M. reticulata* var. *reticulata*
aa. Leaves with long dibrachiate pubescence below, the blades mostly obovate, the apex obtuse ..... 2b. *M. reticulata* var. *rugosa*

2a. **Maripa reticulata** var. **reticulata**

Lectotype: Brazil, Pará, Diamantino, 31.1.1917, *Ducke MG 16719* MG; isolectotypes F, G, US.

Common names: "Cipó abacate" (Ilha de São Luiz de Maranhão—*Froes*); "baboen-malasi" (Jodensavanne, Surinam—*Vreden*); "cipó brasa" (Belém, Brazil—*Oliveira*).

Surinam and Brazil (Amazonas, Maranhão, Pará); forest edge along open area, river edge, forest on terra firme, secondary forest, campo, igapó, capoeira, ilha de mata no campo, mata virgem, savanna forest; flowering November to July; fruiting February to November.

BRAZIL. AMAZONAS: Macapá, Curiaru, beira da floresta ao longo de campo aberto, cipó, frt preto, planta lenhosa, 10.7.1951, *Froes & Black 27387* (IAN). Boca do Acre, Rios Purus and Acre, track from Boca do Acre air-strip to Monte Verde, N bank of Rio Purus on terra firme, liana, frts green, 21.9.1966, *Prance, Penna, Ramos & Videcki 2487* (MG). GOIAS: Rio Corda, afl do Araguaia, região de Xambica, beira do rio, 24.3.1961, *Oliveira 1500* (IAN). MARANHÃO: Alcantara, Periuaçu, 11.4.1954, *Froes 30770* (IAN). São Luíz, floresta secundaria a caminho para o Reservatorio de Sacaven, 27.12.1951, *Froes 27810* (IAN). São Luíz, border of creek, secondary forest, Rio Anil, 10.5.1949, *Froes 24207* (IAN). Estrada do Tirical, ilha de São Luíz, terra firme, high land, rocky soil, old clearing, "cipó abacate," 2.3.1939, *Froes 11541* (A, F, G, MO, NY, U). Isla de São Luíz, Estrada do Olho d'Agua, terra firme, low land, rocky soil, old clearing, vine, 2.3.1939, *Froes 11623* (F, MO, NY, U). Carolina, campo, arbusto erecto, 1.6.1950, *Pires & Black 2552* (IAN). Imperatriz, fazenda Antonio Passarinho, cipó enroscada em arvore pequena, 7.8.1949, *Pires & Black 1738A* (IAN). PARÁ: Belém, I.P.E.A.N., Reserva Mocambo, near border of igapó and terra firme, large vine, 13.5.1969, *Austin 4020* (IAN, MO). Belém, I.P.E.A.N., Reserva do Aurá, on varzea of the Rio Guamá, large vine climbing ca. 35 m, 16.5.1969, *Austin 4022* (IAN, MO). Rivers Mojú and Acará, south of Belém, below Acará, on river bank, frts, 1.6.1969, *Austin & Cavalcante 4071* (MG, MO). Belém, I.P.E.A.N., várzea do Aurá, frts, 23.6.1969, *Austin 4214* (IAN, MO). Belém, várzea do Aurá, climbing ca. 15 m, frts, 26.6.1969, *Austin 4231* (IAN, MO). Belém, várzea do Aurá, vine climbing ca. 30 m, frts 26.6.1969, *Austin 4232* (IAN, MO). Beira do Rio Mojú, Fabrica e cercanias, cipó, frt preto, 1.6.1954, *Black 54-16296* (IAN). São Miguel de Guamá, beira do rio, igapó, 21.8.1948, *Dardano & Black 48-3097* (IAN). Ilha do Maranhão, Anil, capoeira, 4.6.1907, *Ducke MG 559* (photo and fragment F, syntype MG). Santarém, Diamantino, capoeira, cipó grande, fl branca, 31.1.1917, *Ducke MG 16719* (F, MG, US, U). Bragança, silva secundaria, terra firme, fl albis calice purpureo, 7.2.1923, *Ducke RB 18012* (RB, U). Serra de Santarém, mata media da parte inferior, cipó grande, fl branca arroseada, 5.7.1926, *Ducke RB 22517* (G, RB, US). Macapá, ilha de mata no campo, fl branca, 22.4.1926, *Ducke RB 22518* (K, RB, US). Rio Curuating, Planalto de Santarém, cursae ao longo do rio, 3.1955, *Froes 31631* (IAN). Rio Xingú, em frente Souzel, Municipio de Porte de Moz, cipó em touceiras sobre arvores ao longo do barranca da margem do rio, 17.11.1955, *Froes 32335* (IAN). Alto Rio Capím, a beira do rio, mata virgem, terrenos inundaveis, 25.3.1949, *Froes & Pires 24137/49* (IAN, INPA, RB). Marajó, Jutuba, campo, cipó curto, sobre Vites florum,

1.7.1902, *Huber MG 2691* (F, G, MG). Monte Alegre, mata da terra firme, fl alva, 26.3.1924, *Kuhlmann RB 22495* (RB, US). Monte Alegre, Colonia Agricola Major Barata, borda de mata baixa, 10.5.1958, *Lima 53-1503* (IAN). Km 1295 do Rodovia Belém-Brasília, frts pretos, "cipó brasa," 18.2.1960, *Oliveira 529* (IAN). Area do IPEAN, terreno piçarrento, 19.5.1965, *Oliveira 3343* (IAN). Mun. de São Domingos, margem do Rio Guamá, *Silva 577* (IAN).

French Guiana. Anno 1863, *Melinon s. n.* (P).

Surinam. Upper Surinam River, 28.6.1921, *B. W. 5366* (U). Hatramiri, liaan, 18.2.1920, *Gerlings (B. W.) 4564* (A, IAN, NY, RB, US, U). Oever van de Suriname-river bij de (vroom.) plant Libanon, tegenover de monking van Powaka-kreek, liaan tot ca. 9 m, 16.1.1961, *Kramer & Hekking 2646* (NY, U, VEN). Brokopondo district, 4 km E of village Brownsweg, savanna forest, Afterwards Lake, liana, sterile, 17.12.1965, *v. Donselaar 2792* (U). Joden-savanne-Mapanekreek area near camp 8, liana, wood produces on cross-section orange resin in circles, forest along road to Sarwa Creek, sterile, "baboen-malasi," 5.5.1967, *Vreden 11745* (U).

2b. **Maripa reticulata** var. **rugosa** (Ducke) D. Austin, comb. et stat. nov.

Maripa rugosa Ducke, Bull. Mus. Hist. Nat. (Paris), Sér. 2. 4: 747. 1932; Arch. Jard. Bot. Rio de Janeiro 6: 83. 1933.

Lianas; branches angular with striae. *Leaves* with petioles 9–16 mm long; blades ± obovate, 5–10 cm long and 3–7 cm wide, the base acute, the apex acute and slightly mucronate to shortly apiculate, thinly-coriaceous, the secondaries 5–6(–8) pairs; pubescent on lower surface with dibrachiate trichomes. *Inflorescences* axillary, racemose, 2.5–3.5 cm long, 3–7 flowered, the rachis and pedicels rufo-pubescent. *Flowers* with pedicels 4–5 mm long; sepals obovate, the internal slightly longer, or inner and outer equal, 5–6 mm long and 5–7 mm wide, membranaceous, rufo-pubescent at base; corolla campanulate, white, ca. 15 mm long, the lobes ovate; stamens shortly exserted between corolla lobes, the filaments ca. 8 mm long, inserted ca. 3 mm above corolla base, the anthers ca. 3 mm long, ovate, the base sagittate; ovary rotund, ca. 1.5 mm long, ca. 1.5 mm in diameter, glabrous, the style ca. 15 mm long, exserted. *Fruits* globose, 15–20 mm long, 15–20 mm in diameter, rugulose, dark brown to black, shiny, the sepals reflexed to ca. 180°; seeds 1, broad-ellipsoid to globose.

Holotype: Brazil, Amazonas, prope São Paulo de Olivença, 20.8.1929, *Ducke RB 22575* RB; isotypes P (not seen), G, K, U, US.

Known only from the type collection.

This variety is distinguished from the var. *reticulata* by its smaller leaves which have fewer secondary veins, dibrachiate pubescence beneath, and the persistent pubescence on inflorescences and sepals.

3. **Maripa longifolia** Sagot *ex* Hall. f., Bot. Jahrb. Syst. 16: 525. 1893.

Lianas; stems terete, angled, light to dark brown. *Leaves* with petioles 12–20 mm long; blades oblong-elliptic to oblanceolate, 11–18 cm long and 2.5–8.5 cm wide, the base obtuse to acute, the apex acute, shortly acuminate or occasionally retuse, subcoriaceous, the secondaries in 11–13 pairs; stellate trichomes on lower side of leaf along costa, glabrescent. *Infructescences* axillary, racemose, 5–12 cm long; bracts triangular, caducous. *Flowers* unknown. *Fruits* ellipsoid, 20–23 mm long, 13–15 mm in diameter, striate, dark brown, the sepals 5 mm long and 6–8 mm wide, tightly appressed; seeds 1, rotund to wide-ellipsoid.

Lectotype: French Guiana, Karouany, anno 1878, *Sagot 1201* W; isolectotypes B† (photos MO, US), BM, K, U.

I hesitate to recognize this species, but the only known collection cannot be placed in any other. The plant is very similar to *Maripa reticulata* but cannot belong to that species because of the appressed sepals; the sepals of *M. reticulata* are reflexed. The specimens are similar to *M. axilliflora*, but there are no other collections of this species from eastern South America. The fruit shape and leaf texture, while similar to both *M. reticulata* and *M. axilliflora*, differ in several characters. The specimens available may be only a variety of one of these species, but the differences do not permit me to place it in either.

Hallier (1893) and Gleason (1929) have been the only people to discuss this species in publications. In the introduction to his study, Hallier lists twelve herbaria from which he examined material; Berlin, Boissier, the Breslau Museum, Brussels, Copenhagen, De Candolle, Delessert, Florence, Hamburg, the private collection of Prof. Haussknecht, Munich, and Vienna. Of these herbaria I have seen the collections at Berlin, Copenhagen, Geneva, Munich, and Vienna. Only photographs of the Berlin material are now available, the actual material having been destroyed during the Second World War according to Dr. Domke, Director of the Botanical Museum in Berlin (personal communication, 1970). A specimen of *Sagot 1201* was found only in Vienna.

Hallier mentioned *Maripa longifolia* on four pages, 481, 502, 506, and 525. In all these places he discussed only vegetative characters. On page 506 he says "auch bei *Humbertia*, von der mir Samen leider nicht vorlagen, suchte ich in der Achse, sowie im Blatt, Kelch und Fruchtknoten vergebens, und ebenso leiss sich für *Maripa longifolia*, die mir nur steril vorlag . . . ." [I could not detect their (secretory cells) presence in *Humbertia* whose seed I did not have, where I searched the stem, leaf, calyx, and ovary in vain; similarly in *M. longifolia* which lay sterile before me . . . ."]. There is but one specimen that I have seen which could have been seen by Hallier, that deposited in Vienna. This sterile specimen is with little doubt that examined by Hallier, since there is a segment taken from one of the leaf blades and Hallier is the only person known to have examined the species anatomically. Because of these facts, the sterile specimen in Vienna is selected as lectotype. Although sterile, it is easily referable to the species.

4. **Maripa axilliflora** Mart. *ex.* Meisn. *in* Mart., Fl. Bras. 7: 208. 1869.

Murucoa axilliflora (Meisn.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
Maripa maxilliflora Gleason, Bull. Torrey Bot. Club 56: 109. 1929, sphalma.
Dicranostyles kuhlmannii Hoehne, Anexos Mem. Inst. Butantan, Secc. Bot. 1(6): 46, *pl. 6.* 1922. (Type: Brazil, Rondonia, Matto Grosso, *Kuhlmann 2267* SP, not seen, RB.)
Maripa kuhlmannii (Hoehne) Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 589. 1932.
Merremia kuhlmannii (Hoehne) L. Barroso, Rodriguesia 10: 23. 1948.

Lianas; branches terete, green when young. *Leaves* with petioles 15–30 mm long; blades oblong, ovate to elliptic-lanceolate, 10.5–18 cm long and 4–8 cm wide, the base acute to shortly attenuate, the apex acute to shortly acuminate, thin-coriaceous, the secondaries (10–)12–14 pairs; glabrescent. *Inflorescences* axillary, racemose, 4–6 cm long, (6–)10–12(–14) flowered; bracts triangular, to

1.5 mm long, caducous. *Flowers* with pedicels 4–8 mm long, covered with scattered peltate glandular scales; sepals ovate to widely ovate, 5 mm long and 6–7 mm wide, coriaceous, ciliate, glabrous or with scattered peltate glandular scales outside; corolla campanulate to long-campanulate, white, 10–15 mm long, the lobes ovate-oblong, obtuse, deeply incised; stamens exserted at the corolla lobes, the filaments 5 mm long, inserted 2 mm above corolla base, the anthers narrowly ovate, basally sagittate, 4 mm long; ovary rotund, ca. 1 mm long, ca. 1 mm in diameter, glabrous, the style 8–13 mm long, glabrous. *Fruits* ellipsoid, 20–25 mm long, 13–15 mm in diameter, pale shiny brown, the calyx appressed; seeds 1, ellipsoid, 15–20 mm long, ca. 10 mm in diameter.

Lectotype: Peru, San Martin, near Taropoto, anno 1855–56, *Spruce 4230* BR; isolectotypes BM, C, F, G, GH, GOET, W.

Eastern Peru and southwestern Brazil; forest terra firme and lake shores; 200–400 m; flowering October to March; fruiting May to June. Illustration: Fl. Bras. 7: *tab. 73.*

Brazil. rondonia: Matto Grosso, entre os Rios Burití e Formigueiro, arbusto mais ou menos scandens de 3–4 m de alt, fl levemente roxa, 6.1918, *Kuhlmann 2267* (SP n. v., RB).

Peru. loreto: Mischuyacu, near Iquitos, 100 m, forest, liana, fls white, 2–3.1930, *Klug 1074* (F, US). Río Mazan, rising ground, solitary, fls white, 100–125 m, 15.2.1935, *Schunke 258* (A, F, NY, US). Pau-Cocha (Pucallpa), liana 15 m high on shores of the lake, frt almost black, 200 m, 6.5.1961, *Woytkowski 6307* (GH, MO, US). san martin: Juan Jui, alto Río Huallaga, ca. 400 m, forest, liana, fls white and yellow, 10.1934, *Klug 3895* (MO); 1.1936, *Klug 4227* (BM, F, K, MO, US). Iquitos, silva non inundabili, fls albis, 20.2.1924, *Kuhlmann RB 22499* (G, K, U, US). Prope Taropoto, 6.1856, *Spruce 4230* (K).

The plants which have been segregated as *Maripa kuhlmannii* agree with the typical specimens of *M. axilliflora* in all characters except that the flowers are slightly larger and the leaves dry dark brown. This does not seem to merit their exclusion from *M. axilliflora* as a distinct group, and I have included them with this species.

Subg. 2. **Maripa**

Section 1. **Maripa**

5. **Maripa scandens** Aublet, Hist. Pl. Gui. Fr. 1: 230. *tab. 91.* 1775.

Ehretia cirrhosa Lam., Encycl. Méth. Bot. 1: 527. 1783, *non* L., Syst. Veg., ed. 10. 936. 1759.
E. scandens (Aublet) Poiret *in* Lam., Encycl. Méth. Bot. Suppl. 3: 590, 1814. *non* L., Syst. Veg., ed. 10. 936. 1759.
Maripa erecta G. F. W. Meyer, Primit. Fl. Esseq. 115. 1818. (Type: Guyana anglica ad ripas flum. Iterbishicreek, *Rodschied s. n., fide* Meyer, GOET.)
M. cayennensis Meisn. *in* Mart., Fl. Bras. 7: 208. 1869. (Type: Cayenne, French Guiana, *Herb. Kunth* B†; isotypes P, not seen, photos MO, US.)
M. cordifolia Klotzsch *ex* Meisn. *in* Mart., Fl. Bras. 7: 209. 1869. (Holotype: *Schomburgk 1469b* B† (photos MO, US); isotype K.)
M. scandens var. *β cordata* Meisn. *in* Mart., Fl. Bras. 7: 209. 1869. (Type: "in desertis Sinemari, Guyanae gallicae," not seen).
Murucoa cayennensis (Meisn.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
M. erecta (Meyer) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
M. cordifolia (Meisn.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
M. scandens (Aublet) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.

Maripa guianensis Sagot *ex* Gleason, Bull. Torrey Bot. Club 56: 111. 1929, *nom. nud. pro syn.*
M. scandens var. *albicans* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 170. 1925. (Holotype: *Ducke RB 18013* RB; isotypes K, US.)
M. scandens var. *argentea* Benoist, Bull. Mus. Hist. Nat. (Paris) 26: 560. 1920. (Type: *Wachenheim* 44 P, not seen.)
Lysiostyles cayennensis (Meisn.) Roberty, Candollea 14: 41. 1952.

Lianas; stems terete, brownish- to grayish-black, often with white lenticels. *Leaves* with petioles 8–25 mm long; blades broadly ovate to ovate-oblong, (6–)10–18 cm long and 4–9 cm wide, the base cordate, rounded or shortly attenuate, the apex obtuse, acute or acuminate, coriaceous, the secondaries 7–9(–12) pairs; glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, yellowish- to whitish-pubescent; bracts ovate, apically obtuse, persistent, pubescent. *Flowers* with pedicels 2.5–8 mm long; sepals ovate, suborbicular to widely ovate, 5–9 mm long and 4–14 mm wide, coriaceous, both the external and internal lobes with appressed dibrachiate trichomes dense enough to impart a yellowish or whitish color; corolla cylindric-funnelform to funnelform, white to violet or pink, 15–35 mm long, the lobes rotund; stamens included, the filaments 4–11 mm long, inserted 4–6 mm above corolla base, the anthers narrowly ovate, basally sagittate, 3–6 mm long; ovary ovoid to conic, 2–5 mm long, 1.5–2 mm in diameter, the apex glabrous or pubescent, the style 10–20 mm long, pubescent on upper ⅓–½, glabrescent. *Fruits* ellipsoid to ellipsoid-obovoid, 20–30 mm long, 13–20 mm in diameter, smooth to slightly striate, dark brown, often grayish tinged, the calyx tightly appressed around base; seeds 1(–2) ovoid to ovoid-ellipsoid, 15–22 mm long, 10–15 mm in diameter.

Lectotype: French Guiana, Sinnemary River, *Aublet s.n.* BM; isolectotypes P-LAM, not seen, P-DEN, not seen, photo of P-LAM at US.

Common names: "Monkey syrup" (Guyana—*Persaud*, *Sandwith*), "brasa" (Amazonian Brazil—LeCointe, 1947).

Eastern Venezuela, Guyana, Surinam, French Guiana, and Brazil (Amazonas and Pará); terra firme, várzea, igapó, riverside, seasonal pond edge, cloud forest; sea level to 900 m; flowering April to January; fruiting October to April and July to August, but fruits may be found in any month, since they often persist on plant. Illustrations: Small flowered form, Aublet, Hist. Pl. Gui. Fr. 1: *tab. 91.* 1775; large flowered form, Meisner *in* Mart., Fl. Bras. 7: *tab.* 72. 1869.

Brazil. amazonas: Manaus, margem do Igarape da Bolivia, RB-17 km 19, *Coelho & Lima INPA 3209* (INPA, RB). Manaus, Estrada do Aleixo, margem paludosa de um riachinho silvestre, *Ducke 65* (A, F, K, MO, NY, US); *Ducke 65, 2nd* (IAN, MG, US). Manaus, Igarape da Raiz, silva paludosa, *Ducke 103* (A, F, MO, NY, US); *Ducke 103, 2nd* (IAN, MG, US); *Ducke 273* (NY). Manaus, Igarape da Raiz, ad marginem silvae paludosae, *Ducke RB 35585* (G, K, RB, U, US), Manaus, Cachoeira do Mindú, silva paludosa non inundabili, *Ducke RB 24402* (G, K, RB, U, US). Manaus, silva non inundabili, loco humido ad Estrada do Aleixo, frutex robustus alte scandens, fl pallide roseis, 9.11.1931, *Ducke RB 24405* (G, RB, U, US). Rio Capitari, *Froes 26470* (IAN). Rio Urubú, *Froes 25328* (IAN). Munic. Humayata, near Tres Casas, low terra firme, *Krukoff 6394* (BR, F, G, MO, NY, U, US), *6487* (A, BR, F, G, MO, NY, U). Muic. São Paulo de Olivença, basin Belém cr, terra firme, high forest, *Krukoff 8875* (A, BM, BR, F, G, MO, NY, U, US). Manaus, margem do Igarape

da Bolivia, *Luiz & Francisco INPA 3209* (INPA, IAN). Ad Ega (Tefé), alto Rio Negro, 12.1819, *Martius s. n.* (M). Rio Madeira, road Humaita to Labrea km 44, *Prance, Pena & Ramos 3467* (MG). Manaus, km 60 da estrada Manaus—Itacoatiara, *Rodrigues & Lima 2728* (INPA). PARÁ: Belém, S forest of IAN, *Archer 7704*; *Archer 7876* (both IAN). Rio Acará, S of Belém, between Tomé-Acú and Acará, river margin, large vine in tangle, pendant from tree ca. 20 m, 3.6.1969, fr, *Austin & Cavalcante 4106* (MG, MO). Rio Mojú, ca. ⅔ way between mouth and city of Mojú, vine climbing *Alantoma* ca. 20 m on west bank, thick mat of vines pendant into water, fr, 3.6.1969, *Austin & Cavalcante 4129* (MG, MO). Rio Mojú ca. ⅔ way between mouth and city of Mojú, vine climbing ca. 10 m along mat at river edge, on E bank, all fr with side eaten out except one which germinated under water, 3.6.1969, *Austin & Cavalcante 4130* (MG, MO). Road E of Belém, between Castanhal and Igarape Itarumá, vine on tree at edge of igarape, sterile, 18.6.1969, *Austin & Cavalcante 4200* (MO). Belém, várzea do Aurá, vine climbing tree ca. 20 m at edge of igarape, 26.6.1969, *Austin 4234* (IAN, MO). beira do Rio Guamá, acima do São Miguel, *Black & Foster 48-3378* (IAN). Belém, road in front of IAN, *Ducke 7704* (F, NY, US). Belém, S forest of IAN, *Ducke 7876* (F, K, NY). Estrada de Igarape do Cauhy, Faro, *Ducke MG 10562* (MG, RB, US). Belém, *Ducke MG 15551* (MG, RB, US). Ilha de Breves, margem inundavel do Rio Mucujubim, *Ducke RB 12381* (RB). Torto de Moz, *Ducke MG 16656* (MG, RB): Região do Anapu, Rio Maparaua, Portel, *Froes 32707* (IAN). Portel, *Froes 32783* (IAN) Bragança, *Huber 1709* (MG, RB). Rio Arama, *Huber MG 1843* (MG, RB, US). Rio Jarí, planalto de Monte Dourado, *Oliveira 3961* (IAN). Rio Jarí, Porto Munguba, *Oliveira 3510* (IAN). Belém, mata virgem da Agua Preta, *Pires & Black 360* (GH, IAN). Ilha de Marajó, Breves, *Pires & Silva 6679* (IAN). Belém, IPEAN, *Pires & Silva 10843* (IAN). Belém, Reserva Aurá, *Pires & Silva 11355* (IAN). Belém, Igapó do Catú, *Pires & Silva 11414* (IAN). Belém, near São Joaquim, *Silva 157* (IAN). Belém, mata do Cafezal, *Silva 190* (IAN). Santarém, Rio Maica, *Silva 1393* (MG). GUANABARA: Horto no Jardim Botanico de Rio de Janiero, *Porto RB 81817* (RB). RONDONIA: Upper Machado Rio region, near Tabajará, terra firme, fl grayish, 11–12.1931, *Krukoff 1320* (A, F, G, MO, NY, U).

FRENCH GUIANA. Montagne de Kaw, fl pink-violet, locally occasional in trees at edge of dry seasonal pond, 250 m, 14.12.1954, *Cowan 38838* (K, NY). Anno 1802, *Gabriel* (F, G). Anno 1859, *Leprieur 216* (F, G); *Leprieur 271* (G, P); *Leprieur 1460* (G). Anno 1838, *Leprieur s. n.* (P). Cayenne, *Martin 238* (G), *s. n.* (K). Piamens, Mout Fissery, belle liane, 3.1840, *Melinon 81* (P); *Melinon 123* (BM, K). Maroni River, *Melinon 378* (BM, F, K, NY, US). Anno 1863, *Melinon* (BM, F, G, GH, NY, US). Anno 1864, *Melinon* (BM, GH, NY, US). Anno 1866 *Melinon* (P). Anno 18??, *Melinon s. n.* (P). Cayenne, *Moricand 2* (G); *Perrottet 241* (F, G), *292* (G), *233* (G); *Poiteau 1461* (G). Oyapoek, 25.12.1948, *Rue 20* (P); *Sagot 379* (BM, G, K, U, W). Cayenne, *Sagot s. n.* (P). Ile Portal, Bar, ex herb. *Sagot s. n.* (P). Riviere de Kourouy, grand bois 3.1877, *Jbrevame*(?) *s. n.* (P). Crevaux, Kourau, *leg. ign. s. n.* (P).

GUYANA. Mazaruni River, Lalacoon, *Aelson 32* (K), Manaka, over riverine growth, *Atkinson 21* (BM, US). Upper Rupununi River, near Dadanawa, *De La Cruz 1372* (F, MO, NY, US), *1538* (F, GH, MO, NY, US). Wamamuri Mission, Moruka River, Pomeroon distr., *De La Cruz 2515* (F, GH, MO, NY, US). Malali, Demarara River, *De La Cruz 2635* (F, GH, MO, NY, US). Kamakusa, upper Mazaruni River, *De La Cruz 2811* (GH, NY, US), *2837* (F, GH, MO, NY, US). Pomeroon River, 18 feet tall, fl yellow, *De La Cruz 3183* (F, NY). Kaietur Falls, Potaro River, *De La Cruz 4412, 4483* (both F, GH, MO, NY, US). Winiperu Creek, Essequibo River, a tough grey-black rope from the crown of a *Mora* in mixed forest on brown sand, *For. Dept. Br. Gui. 281(3017)* (K, JENM). Labbakabra Creek, Essequibo River, climbing to crowns of large trees in miscellaneous forest, *For. Dept. Br. Gui. 327(3063)* (K). Vicinity of Kartabo Station, junction Mazaruni & Cuyni Rivers, *Graham 123* (NY). Youly-Niby, *Hancock 96* (K). 2 miles E Atkinson Field, in damp humid vale, sandy soil, *Irwin BG-60, BG-61* (both US). Corentyne River, ?*Jenman 20* (K). Mazaruni River, of trailing or subtrailing habit, *Jenman 695* (K). Demarara River, *Jenman 4874* (BM). ?Macouria River, *Jenman 2500* (K). Kow Island, Essequibo River, *Jenman 7639* (K, U). Kurupung Sacoba, *Lang & Persaud 211* (F). Upper Mazaruni River, Kamakusa, climbing 40 feet, stems 3 inches in diameter, *Leng 64* (NY). Matthews Ridge, Barima River, *Maguire 40511* (F, NY, RB, US). Upper Essequibo River, near Ororo, large liana in riverbank curtain, *Meyer 5722* (K). Maritaro, *Persaud 123* (F, NY, U). Demarara River, *Persaud 195* (F). Essequibo River, Moraballi Creek, near Bartica, mixed forest, frequent, *Sandwith 506* (K, NY, RB, U, US), *600* (K, NY, RB, U); *Schomburgk 110(46)* (G, K, W), *1496b* (K).

SURINAM. Blakawatra, bij Jodensavanne, *Boerleoorn 8775* (U). Sectie O, *B.W. 346* (BR). Coppename River, Raleigh falls, *B.W. 6172* (RB, NY). Placer Lawa, Lawa River, *Gonggrijp (B.W.) 4159* (U, US); *Gonggrijp & Stahel 346* (U); *Hostmann 1293* (U); *Hostmann & Kappler 1251* (BM, G, GH, K, MO, NY, W). Afobaka, district of Brokopondo, *Kramer & Hekking 2833* (NY, U). In montibus, qui dicuntur Nassau, bergsavanne bos bij km 5.9, *Lanjouw & Lindeman 2415* (K, NY). Fluv. Saramacca sup. pr Janbasigado, *Pulle 404* (U). SW of village Brokopondo, *v. Donselaar 2806* (BR, F, U). Fluv. Litanie sup. pr Mount Knopaiamoi, *Versteeg 391* (U). Ca. portum aeronaut. ad flum. Oelemari, *Wessels Boer 1141* (A, U). In ripas flum. Suriname super., Jodensavanne, *Wullschlägel 821* (BR, GOET, NY, W). Boven-Suriname River, bij Goddo, *coll. indig. U 07490* (U).

VENEZUELA. AMAZONAS: Yavita, bejuco leñoso sobre los ramas de arboles altos en la selva tupida, 128 m, *Williams 13949* (F, G, RB, US, VEN, W). BOLIVAR: Valle boscoso (denominado localmente Parakaupa), NE de Canaima, 200–500 m, *Agostini 342* (VEN). Woods along trail between campamento Los Vaquiros & El Cruzero, altitude 300 m, *Steyermark 86329* (VEN). Along Río Reforma above junction with Río Toro, Sierra Imataca, *Steyermark 87946* (VEN). Rainforest between junction with Río Reforma and 1 km below junction with Río Toro, *Steyermark 88138* (NY, U, VEN). Cerro El Picacho & vicinity N of Las Cicharras, 45 km N of Tumeremo, Altiplanicie de Nuria, 620 m, *Steyermark 89030* (VEN). Cloud forest on summit of SE-facing escarpment, E of Cerro El Pichacho, N of Las Nieves & Las Chicharras, N of Tumeremo, vicinity of Deborah, 600–650 m, *Steyermark 89122* (NY, VEN). Cabaceras de Río Chicanan, 80 km SW de El Dourado, altitude 700 m, *Steyermark 89395, 89474* (both NY, VEN). Cerro Venamo, entre la ladera principal escarpada de arenisca y el salto en Río Venamo, 900–1000 m, *Steyermark, Dunsterville & Dunsterville 92844* (MO, U, VEN). DELTA AMACURO: Primary forest near Río Grande, E of Upata, *Bruijn 1673* (VEN). Río Amacuro, Sierra Imataca, downstream from San Victor, 65–80 m, *Steyermark 87306* (NY, U, VEN). Río Cuyubini, Cerro La Paloma, Sierra Imataca, 100–200 m, *Steyermark 87601* (NY, VEN). Bosque pluvial E de Río Grande, 36.5 km NE de El Palmar, ca. de los limites del Estado Bolívar, 320 m, *Steyermark 93149* (MO, VEN). MIRANDA: Parque Nacional de Guatopo, 600–700 m, *Steyermark 90099, 97547* (both VEN). SUCRE: Peninsula de Paria, Cerro Patao, N de Puerto de Hierro, NE de Güiria, 870 m, *Steyermark & Agostini 91347* (US, VEN). Peninsula de Paria, Cerro de Humo, a lo largo de las cabeceras de Río Santa Izabel, 700–800 m, *Steyermark & Rabe 96328* (MO, VEN).

The range in flower size has long caused difficulties in the interpretation of this polymorphic species. Many authors have dismissed the apparent differences between Aublet's drawing and the majority of material collected with a reference to the notoriety for inaccuracy which Aublet has achieved. The present case is one where Aublet has been unjustly criticized. Except for the stamens, which are drawn opposite the corolla lobes instead of alternate with them, the plate he provided for this species is quite accurate. It is so accurate that the specimen in the British Museum is with little doubt that which formed the basis for the habit part of Aublet's drawing. Aublet's plate is a composite with the young fruits on the habit sketch, the inset of young fruits, and the dissection of flower parts being taken from material which, at least at present, does not accompany the specimen at the British Museum. The tendril (including the number and direction of curls), the leaves, and the curve of the branch all match the specimen at the British Museum (Fig. 36–37).

Collections of this species show a wide range in size and in indument pigmentation. These variables have prompted many different interpretations as shown in the synonymy list. Choisy (1845) was apparently the last person to correctly apply Aublet's name to the small form. Other authors saw mostly large flowered material, applied Aublet's name to that, and established new names (*Maripa cayennensis, M. cordifolia*) for the small flowered form. The

FIGURES 36–37.—36. Plate of *Maripa scandens* published by Aublet (1775).—37. Lectotype of *Maripa scandens* collected by Aublet and deposited in BM.

disparity between the majority of plants available and Aublet's illustration was often noted but ignored, or dismissed with the statement that "Aublet's illustrations are notoriously inaccurate and his descriptions usually omit or neglect the characters now known to be of chief taxonomic value . . ." (Gleason, 1929: 108).

An examination of large quantities of material of this species has shown that both the large and small flowered forms may have either white or yellow indument and that the apparent size differences are inconsistent. It is possible to find buds of quite different sizes on the same branch, although this is not common. The extremes may be easily separated by size, but there are many specimens which cannot be placed in one group or the other. It is impossible to say whether fruiting specimens should be referred to the small or large flowered form, since there seems to be no correlation between flower size and fruit size.

Moreover there is apparently no correlation between distribution and the size differences in this species. Small flowered forms have been collected from the Guianas to the border between Peru and Brazil. Collections by Ducke (*Ducke* 65 and *Ducke* 65, *2nd*) suggest that flower size may vary considerably from one year to another. The variation in sepal size does not seem to be as great, but it also seems variable. Clearly the factors influencing size differences in this species are in need of further examination.

See *Maripa janusiana* for relations and similar species.

6. **Maripa densiflora** Benth., London Jour. Bot. 5: 351. 1846.

Murucoa densiflora (Benth.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.

Lianas; stems terete, angled to smooth, light to dark brown. *Leaves* with petioles 10–30 mm long; blades ovate to oblong-elliptic, 6.5–20 cm long and 4–11 cm wide, the base obtuse to rounded, the apex shortly acuminate, coriaceous, the secondaries 8–13 pairs; glabrescent above, densely glandular pubescent below. *Inflorescences* terminal, paniculate-thyrsiform; bracts triangular to ovate-triangular, to ca. 1.5 mm long, acute, mostly persistent at anthesis, some persistent in fruit, ciliate, with peltate glandular indument. *Flowers* with pedicels 3–6 mm long; sepals ovate to broadly ovate, the outer 4–5 mm long, the inner 5–6 mm long and 5–7 mm wide, coriaceous, ciliate, outside of external sepals with glandular peltate indument, interior sepals with appressed indument outside; corolla cylindric-funnelform, white to pinkish, 15–18 mm long, the lobes obtuse to rounded; stamens included, the filaments 5 mm long, inserted 3 mm above corolla base, the anthers narrowly ovate, basally sagittate, 4–5 mm long; ovary conic-oblong, 4 mm long, ca. 1.7 mm in diameter, the base glabrous, the apex densely villose with a beard about as long as the glabrous base, rarely glabrous, the style 11–12 mm long. *Fruits* ellipsoid to oblong-ellipsoid, 27–30 mm long, 10–16 mm in diameter, slightly flattened, the surface with numerous small striae, dark brown, often with villose apiculum, the calyx tightly appressed against fruit base; seeds 1, flattened, oblong to ellipsoid, ca. 20–25 mm long, ca. 8–12 mm in diameter.

Holotype: Brazil, Amazonas, Rio Padawire, *Schomburgk 232.5* K.

Rio Negro and Rio Cassiquiare areas of Brazil and Venezuela; igapó, várzea, and river islands; flowering November and December; fruiting in February.

BRAZIL. AMAZONAS: Upper Rio Negro, Ilha Nova Vida, 12.2.1944, *Baldwin 3287* (IAN, US). Rio Negro, Santa Izabel, silva riparia periodice inundata, fl albis, 12.11.1929, *Ducke RB 22573* (K, RB, U, US). Rio Curicuriary, affluent Rio Negro, fl roseo pallido, encima das cachoeiras, praia baixa, 25.11.1936, *Ducke RB 35584* (RB). Rio Negro, Cucui, igapó, fl branca-arroxeada, 3.11.1962, *Rodrigues & Coelho 4785* (INPA). Secus Rio Negro, inter Barcellos et San Gabriel, 12.1851, *Spruce 1928* (BM, BR, F, G, K, MO, NY, RB, W).
VENEZUELA. AMAZONAS: São José de Cassiquiare, *Froes 21502* (IAN, K, MO).

The indument of *Maripa densiflora* is more variable than for any other species. There are almost no peltate glandular trichomes on the Schomburgk and Spruce collections, while the inflorescences of the Ducke collections are heavily covered with this kind of pubescence. The fruits on the collection by Baldwin shown an apiculum which is heavily bearded, but in the Froes collection the ovary is glabrous while still in flower.

See *Maripa janusiana* for relations.

7. **Maripa janusiana** D. Austin, sp. nov.

Maripae densiflorae simili, sed trichomatibus dibrachiatis ramis aequalibus, sepalis aequalibus et in alabastris appresis, 2–3 mm minoribus, ovariis glabris, et foliis leviter tenuioribus differunt.

Lianas; stems light brown to brown, striate or smooth. *Leaves* with petioles 10–15(–20) mm long; blades ovate, elliptic-ovate to oblong, (7–)12–25(–37) cm

long, the base obtuse, slightly cordate to acute, the apex acute to shortly acuminate, occasionally obtuse to retuse, coriaceous, the secondaries 7–11 pairs; densely peltate glandular below. *Inflorescences* terminal, paniculate-thyrsiform, glabrous except for small peltate glandular trichomes; bracts ovate-triangular to ovate, to 2 mm long, ciliate, with scattered peltate indument. *Flowers* with pedicels 4–6 mm long; sepals broadly ovate to subrotund, 4–5 mm long and 5–6 mm wide, the external lobes coriaceous, the internal lobes membranaceous, ciliate, the external lobes glabrous, the internal glabrous or sparsely pubescent outside; corolla funnelform, lilac to violet, 18–20 mm long, the lobes rotund; stamens included, the filaments 4–5 mm long, inserted 4 mm above corolla base, the anthers narrowly ovate, basally sagittate, 4–5 mm long; ovary oblong-conic, 2–2.5 mm long, ca. 1.5 mm in diameter, glabrous, the style 12–13 mm long. *Fruits* ellipsoid, 25 mm long, 12–13 mm in diameter, brown, the calyx appressed to base, supporting; seeds 1, ellipsoid, 11 mm long, 8 mm in diameter.

Holotype: Peru, Loreto, Mischuyacu, *Klug 809* US; isotype F (Fig. 41).

Eastern Peru and western Brazil; forest, high forest, terra firme; altitude 100 m; flowering October to January.

BRAZIL. AMAZONAS: Munic. São Paulo de Olivença, Belém cr, basin Rio Solimões, terra firme, high forest, vine, *Krukoff 8634* (A, BM, BR, F, G, MO, NY, U), *8707* (A, BM, F, G, MO, NY, US, U).

PERU. LORETO: Mischuyacu, near Iquitos, altitude 100 m, forest, 10.11.1929, *Klug 590* (F, US). Prov. Maynas, alto Nanay, 6.3.1968, *Simpson & Schunke 807* (FAU, F).

This species is named after the Roman deity Janus who, like the trichomes on this plant, faced in two directions.

Maripa janusiana is a member of the section *Maripa*, which contains the most difficult group of species in the genus. They all differ by subtle, but constant characters. I have examined living plants of both *M. glabra* and *M. paniculata*; differences become much more apparent when they are alive. *Maripa glabra* and *M. paniculata* are easily separated by either the presence (*M. glabra*) or absence (*M. paniculata*) of oil glands on the upper leaf surface. The latter species also usually has a few trichomes near the apex of the style. *Maripa janusiana* is quite similar to *M. densiflora*, which is similar to *M. scandens*. *Maripa janusiana* is easily distinguished by the dibrachiate corolla trichomes with branches of equal length. The species is unique in the genus for this character. However, these trichomes are similar to those in some species of *Dicranostyles*. *Maripa densiflora* is the only species in the genus with markedly unequal sepals. *Maripa densiflora* and *M. scandens* are easily separated by the pubescent sepals of the latter species.

The differences in all these species become more apparent in fruiting material; yet all the species must be closely related and quite homogeneous except for *M. williamsii*, which is somewhat intermediate between sect. *Maripa* and sect. *Mouroucoa*.

8. **Maripa paniculata** Barb.-Rodr., Vellosia, ed. 2. 1: 59, *pl. 16*. 1891.

Lianas; stems terete, somewhat rugose. *Leaves* with petioles 7–30 mm long; blades ovate, oblong or elliptic, 5–18(–28.5) cm wide, the base obtuse, the apex

acute to shortly acuminate, occasionally retuse, coriaceous, the secondaries (6–)7–8(–11) pairs; glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, the rachis glabrous, the branches pubescent; bracts oval, the apex acute, persistent, ciliate, pubescent. *Flowers* with pedicels 3–8 mm long; sepals oval to rotund, 4–5 mm long and 5–6 mm wide, ciliate, pubescent on external surfaces; corolla cylindric-funnelform, violet, 17–20 mm long, the lobes obtuse; stamens included, the filaments 6 mm long, inserted 3–4 mm above corolla base, the anthers oblong, basally sagittate, ca. 4 mm long; ovary conic, ca. 2 mm long, ca. 1.5 mm in diameter, glabrous, the style ca. 10 mm long, pubescent on upper half. *Fruits* ellipsoid, 30–35 mm long, ca. 15 mm in diameter, smooth to slightly rugose, brown, shiny, the sepals loosely appressed; seeds 1, ellipsoid, ca. 20–30 mm long, ca. 12 mm in diameter.

Holotype: Brazil, Amazonas, Rio Negro, prope Manaus ad ripas Igarape do Aterro, *Barbosa-Rodrigues* 368 Herb. Mus. Bot. Amaz.-Manaus†?; the plate will have to be chosen as the type, if the specimen is proven destroyed.

Common names: "Brasa" (Manaus, Brazil—*Huber*), "moo-se-ree-ha" (vine-of-cricket) (Colombia—*Schultes & Cabrera*).

The Amazon and Rio Negro Basins of Colombia, Peru, and Brazil; capoeira fechada de terra firme, mata virgem, ad ripas paludosas; 100 m; flowering June to November; fruiting in October. Barbosa-Rodrigues illustrated the species; however his plate does not show most of the characters needed for determination.

BRAZIL. AMAPÁ: Rio Araguari, vicinity of camp 12, petals white, upland plant, 2.10.1961, *Pires, Rodrigues & Irvine 51443* (IAN). AMAZONAS: Manaus, km 19 da BR-17, capoeira fechada, terra firme, arenoso, fls alvo-arroxeadas, 15.9.1955, *Chagas INPA 1913* (INPA, MG). Esperança, mata da terra firme, corolla roseo muito pallido, 5.2.1942, *Ducke IAN 127* (IAN). São Paulo de Olivença, silva non inundabili, fls pallide rosei fere albi, 21.11.1940, *Ducke 643* (F, IAN, K, MO, NY, US). São Paulo de Olivença, corolla alba, 6.10.1931, *Ducke RB 24406* (K, RB, US); Esperança, ad ostium Javary, fls pallide roseis, 23.9.1931, *Ducke RB 24407* (RB, U). Manaus, silva humosa regione fluminis Taraumã superioris, terra firme entre as duas cachoeiras dos Rios Tarumã, fls pallide roseis, 17.9.1929, *Ducke RB 22576* (RB, U). Manaus, ad ripas paludosas rivuli Igarape da Raiz, fls, 19.10.1929, *Ducke RB 22577* (G, RB, US). Rio Capitari, terra firme alta, floresta alta, fls, 3.9.1950, *Froes 26542* (IAN). PARÁ: Rio Una, região do Planalto de Santarém, 30.7.1955, *Froes 32011* (IAN). Igarape de Lama, planalto de Santarém, mata virgem, 7.1954, *Froes 30983* (IAN).

COLOMBIA. AMAZONAS: Río Apaporis, Jingoje at mouth of Río Piraparana & vicinity, 700 feet, frt brown, 15.6.1952, *Schultes & Cabrera 16740* (BM, U).

PERU. AMAZONAS: Mouth of Río Santiago, *Tessmann 4440* (NY). LORETO: Iquitos, loco Huyabamba, fls albis vix subviolascentibus, 13.11.1945, *Ducke 1849* (A, F, MG, NY, US). Near Iquitos, Mischuyacu, 100 m, forest, fls bright lilac, 10–11.1929, *Klug 72* (F, US). Near Iquitos, Mischuyacu, *Klug 562* (F, US).

See *Maripa janusiana* for relations.

9. **Maripa glabra** Choisy *in* DC., Prodr. 9: 327. 1845.

Gaseranthus glabra Poiteau *ex* Meisn. *in* Mart., Fl. Bras. 7: 206. 1869. (Lectotype: French Guiana, Cayenne, *Poiteau s. n.* G; isolectotypes K, W.)
Murucoa glabra (Choisy) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
Maripa tenuis Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 249. 1922. (Lectotype: Brazil, Pará, Belém, Utinga, 9.7.1914, *Ducke MG 15355* MG; isolectotypes F, G, RB, US.)

Lianas; stems terete when mature, compressed when young. *Leaves* with petioles 8–10(–15) mm long; blades elliptic to ovate-elliptic, 8–17 cm long and

3–10 cm wide, the base obtuse, the apex acuminate, coriaceous, the secondaries (7–)8–10(–11) pairs; with numerous sunken oil glands above, especially prominent near base of blade. *Inflorescences* terminal, paniculate-thyrsiform, cylindric or subcorymbose; bracts oblong, 2–2.5 mm long, persistent. *Flowers* with pedicels 3–4(–7) mm long; sepals suborbicular, 4–5 mm long and 4–6 mm wide, the exterior lobes glabrous, the interior lobes appressed pubescent outside; corolla cylindric-funnelform, white, 15–23 mm long, the lobes rotund; stamens included, the filaments 3–4 mm long, inserted ca. 4 mm above corolla base, the anthers oblong, basally sagittate, 3–4 mm long; ovary conic, ca. 2 mm long, ca. 1.5 mm in diameter, glabrous, the style 9–10 mm long. *Fruits* long-cylindric to ellipsoid, 25–27 mm long, 12–18 mm in diameter, smooth-rugose to slightly striate, brown, the sepals loosely appressed; seeds 1, oblong to oblong-ellipsoid or oblong-cylindric, ca. 20 mm long, ca. 10–15 mm in diameter.

Lectotype: French Guiana, Cayenne, anno 1789?, *leg. ign. 34* G-DC, not seen, IDC-micro fisch seen; photos MO, NY, US.

Surinam, French Guiana, and Brazil (Amapá, Pará, and Amazonas); virgin forest, capoeiras, terra firma, igapó, wet stream sides; flowering June to October; fruiting December to May.

BRAZIL. AMAPÁ: Coastal region, Colonia do Torrão, fls pale pink, infrequent in high forest, 28.8.1962, *Pires & Cavalcante 52606* (IAN, MG). Rio Araguari, vicinity of camp 12, fls white, upland plant, 30.9.1961, *Pires, Rodrigues & Irvine 51377* (IAN, MG). *Pires, Rodrigues & Irvine 51443* (MG). AMAZONAS: Prope Ega do alto Amazonas, 12.1819, *Martius s. n.* (M). Manaus, km 55 da BR-17, terra firme, solo argiloso, fls alvas, 25.8.1961, *Rodrigues & Coelho 2388* (INPA). Estrada Manaus—Itacoatiara, *Rodrigues & Coelho 3188* (RB). Estrada Manaus—Itacoatiara, km 90, Rio Preto, fls roxas e brancas, *Rodrigues & Lima 2202* (INPA, MG). PARÁ: Belém, S forest of IAN, 16.11.1942, *Archer 7823* (IAN). Belém, Reserva Mocambo, terra firme, vine, frts green, 13.5.1969, *Austin 4018* (IAN, MO). Belém, Reserva Mocambo, terra firme, vine, 13.5.1969, *Austin 4019* (IAN, MO). Belém, Reserva Mocambo, terra firme near igapó, sterile, *Austin 4038* (MO). Belém, Reserva Mocambo, igapó do Catú beside Igarape de Agua Preta, vine climbing ca. 20 m, fls white, 20.5.1969, *Austin 4040* (IAN, MO). Belém, near Reserva Mocambo, igapó, vine in fallen tree, frts dark, 20.5.1969, *Austin 4042* (IAN, MO). Belém, várzea do Aurá, border of várzea, edge of Igarape Sapocaia, vine, frts dark, 16.5.1969, *Austin 4021* (IAN, MO). Border between IPEAN and Utinga, terra firme, capoeira fechada, vine, frts dark, 24.6.1969, *Austin 4215* (IAN, MO); growing from old base on fallen tree, sterile, *Austin 4216* (MO); in fallen tree, frts black, much branched near base, many adventitious roots, *Austin 4217* (IAN, MO); small vine sprouted from old cut stem, sterile, *Austin 4220* (MO); small vine ca. ½ inch in diameter, sterile, *Austin 4221* (MO); small vine ca. 3 m long, ca. 1 cm in diameter, growing from well established root system, sterile, *Austin 4222* (MO); vine climbing ca. 20 m, base 7–10 cm in diameter, frt dark, *Austin 4223* (MO); old mata being cut, small vine ca. 1 cm in diameter, fallen with an *Eschweilera odora*, frt black, *Austin 4224* (IAN, MO). Belém, *Dahlgren & Sella 681* (F, NY). Belém, Entroncamento, fl albis, 26.6.1945, *Ducke 1718* (A, F, IAN, K, MG, NY, US). Belém, Murutucu, 1.1902, *Ducke 2596* (MG). Belém, 27.6.1923, *Ducke RB 18011* (B† (photos at MO, US), G, NY, RB, U, US). Rio Guajará, *Froes 32047* (IAN). Rio Guripi, frts, terreno baixo, mata virgem, 17.3.1958, *Froes 34225* (IAN). Igarape de Lama, planalto de Santarém, 7.1954, *Froes 30983* (IAN). Belém, escandente da mata, fls lilazes, 6.8.1955, *Macedo 3994* (IAN, US). Km 177 da Rodovia Belém-Brasília, fls brancas, 8.5.1960, *Oliveira 696* (IAN). Km 174 do Rodovia Belém-Brasília, mata, terreno alagado, beira da igarape, 26.5.1960, *Oliveira 820* (IAN). Estrada de Benfica, estrada de ferro de Bragança, *Oliveira 3264* (IAN). Belém, fls brancas, 6.8.1946, *Pires 639* (INPA, IAN, NY, US). Mata da Cia Pirelli, Fazenda Uriboca, *Pires 6821* (IAN). *Pires 6938* (IAN). Belém Entroncamento, terreno silicoso. fls brancas, 26.6.1945, *Pires & Black 1* (IAN, RB, U). Rio Guamá, IAN, 6.5.1947, *Pires & Black 1564* (IAN, RB). Km 100 da Rodovia Belém-Brasília, fl branca, 21.7.1960, *Silva 581* (IAN). Igarape Una, várzea, Blüte weiss, am Grunde rotbraun, 28.6.1923,

Snethlage 100 (F). Santa Izabel, 6.1908, *Pessoal do Museu MG 9421* (F, MG). Bragança, igapó, 5.12.1908, *Pessoal do Museu MG 9814* (F, MG, US). Santa Izabel, chemin de fer de Bragança, 2.1.1909, *Pessoal do Museu MG 10147* (F, G, MG, US).

French Guiana. 14–16 miles from St. Laurend on road to Cayenne, frts pale green, infrequent in forest, 20.12.1954, *Cowan 38909* (NY). Rio Oiapoque, 2 km N mouth of Rio Iaue, fls weakly fragrant, corolla white, anthers yellow, in forest trees, 25.8.1960, *Irwin, Pires & Westra 47809* (IAN, MG). Near first cachoeira on Rio Iaue, 0.5 km E of confluence with Rio Oiapoque, occasional, 23.8.1960, *Irwin & Westra 47759* (IAN, MG, U, US). Ca. 1 km S mouth Yaroupi River, occasional, 24.9.1960, *Irwin, Pires & Westra 48448* (G, GH, IAN, MG, NY, U, US). Mana, anno 1854, *Melinon 141* (BM, US). Anno 1862, *Melinon 417* (P). Anno 1862, *Melinon* (P). Anno 1863, *Melinon* (F, G, K, P). Anno 1863, *Melinon 83* (P). 1863, *Melinon 447* & *396* (P). Anno 1864, *Melinon 523* (F, NY). Anno 1864, *Melinon* (BM, F, G, GH, NY, P, US). Anno 1819–21, *Poiteau 240* (G). Maroni, anno 1857, *Sagot 1398* (K, U, W); 14.7.1921, *Wachenheim 344* (P). Godebert, *Wachenheim 360* (P); 23.6.1921, *Wachenheim 397* (P); 13.7.1921, *Wachenheim 524* (P).

Surinam. Lelyderp, Jaraweg, 7.9.1922, *Dalger* (*B.W.*) 5985 (U). Patrick Savanne, *Gonggrijp s. n.* (U). Ad ripas flum. Marowyne media, arbor, fls albis, *Kappler 2011* (G, P, U). Brokopondo district, Brownsweg, ad viam ferraem pr km 115–116, seasonal forest by trail to Mazaronitop, ca. 1 km from Br., frt green 5.4.1961, *Kramer & Hekking 3201* (NY, U). Jodensavanne-Mapane Creek area, Suriname River, in hoog bos bij kamp 12, vrucht groene, 19.3.1933, *Lindeman 3550* (U). Voltzberg (foot), virgin forest, fls white, 20.9.1933, *Lanjouw 915* (BR, K, MO, NY, U). In montibus, qui dicuntur Nassau, in forest near km 9, 19.2.1949, *Lanjouw & Lindeman 2199* (K, NY, U). Coppenam River headwaters, fls pale blue, low forest, 28.7.1944, *Maguire 24194* (F, GH, MO, NY, RB, U, US, VEN). Vicinity of Moengo, Cottica River, Moengo-Albina Road, 20.3.1955, *Maguire 40830* (NY, U). Jodensavanne-Mapane Creek area, Suriname River, rain forest, corolla white, 3.9.1956, *Schulz 7751* (MO). Flum. Suriname, pr Sintiadam, Boem, Oeverveget, 25.8.1908, *Tresling 378* (U). Brokopondo district, N village Brokopondo, high forest, *v. Donselaar 3122* (U). Brownsburg, bloemknoppen licht violet, 6.9.1915, *B.W. 768* (U). Prope Guyana, 14.4.1910, *coll, indig. 109* (U).

See *Maripa janusiana* for relations.

10. **Maripa williamsii** v. Ooststr., Recueil Trav. Bot. Néerl. 30: 196. 1933.

Lianas; branches lightly striate, yellow to gray-brown. *Leaves* with petioles 6–11(–20) mm long; blades oblong-ovate, oblong-elliptic to oblong, 6–16 cm long and 3–7 cm wide, the base cuneate, the apex acute to abruptly short acuminate, subcoriaceous, the secondaries in 7–11 pairs. *Inflorescences* terminal, paniculate-thyrsiform; bracts triangular to ovate-lanceolate, 1–2.5 mm long, acute. *Flowers* with pedicels 2–3 mm long; sepals ovate to widely ovate, 4–5 mm long and 4–5 mm wide, glabrous except for the ciliate margins; corolla cylindric-funnelform, 18 mm long, the lobes obtuse to rotund; stamens included, the filaments 5 mm long, inserted 5 mm above corolla base, the anthers narrowly ovate, basally sagittate, 4 mm long; ovary cylindric to cylindric-conic, 2 mm long, ca. 1 mm in diameter, glabrous, the style 12 mm long, glabrous. *Fruits* subglobose to widely ellipsoid, 15–16 mm long, 13 mm in diameter, dark brown to shiny, the calyx slightly divaricate, supporting; seeds 1, ellipsoid, 10–11 mm long, 8 mm in diameter.

Lectotype: Peru, Loreto, Yurimaguas, 23.1.1929, *Williams* 3935 F; isolectotype U.

Loreto, Peru; forest edge; altitude 155–900 m; flowering October to November; fruiting December.

Peru. loreto: Yurimaguas, Río Huallaga, liana vila da mata, 2.11.1924, *Kuhlmann 1368* (RB). Yurimaguas, lower Río Huallaga, edge of forest, 155–210 m, 24.10.1929, *Williams 4023*

(syntypes F, G); 4.4.1929, *Williams 4524* (syntype F); 7.11.1929, *Williams 4710* (F). SAN MARTIN: Taropoto, vine, alto Río Huallaga, 360–900 m, 23.12.1929, *Williams 6621* (syntypes F, G).

Maripa williamsii is similar to *M. glabra* and *M. paniculata*. The oil glands in the leaves of *M. glabra* readily distinguish it from *M. williamsii*; the pubescent sepals of *M. paniculata* differ from the glabrous sepals of *M. williamsii*.

All species of sect. *Maripa* except *M. williamsii* have ellipsoid fruits; *M. williamsii* has subglobose to widely ellipsoid fruits. The shape of fruits in the Convolvulaceae is normally dictated by the number of seeds reaching maturity. Although only one seed per fruit has been found in the fruiting collections of *M. williamsii*, the fruit shape is similar to those species with more than one seed normally developing.

This species is somewhat anomalous in sect. *Maripa* in other characters also. The pollen is extremely variable in the number of colpi present, being almost all 3-colpate in one plant and about equal numbers of 3-colpate, 3 × 3, and 3 × 3 × 3 colpate in another. The leaf venation patterns are not like those of the core members of sect. *Maripa* but more like those of subg. *Ripama*, and the genera *Dicranostyles* and *Lysiostyles*.

Section 2. **Mouroucoa** (Aublet) D. Austin, stat. nov.

Mouroucoa Aublet, Hist. Pl. Gui. Fr. 1: 141. 1775, as genus.

Subsection 1. **Mouroucoa**

11. **Maripa violacea** (Aublet) v. Ooststr. *ex* Lanjouw & Uittien, Recueil Trav. Bot. Néerl. 37: 153. 1940.

Mouroucoa violacea Aublet, Hist. Pl. Gui. Fr. 1: 141, *tab.* 54. 1775. (Lectotype: *Aublet s. n.* P-LAM, not seen, isotype BM.)
Convolvulus macrospermus Willd. *in* L., Sp. Pl. 1(2): 860. 1797.
Maripa passifloroides Benth. *ex* Meisn. in Mart., Fl. Bras. 7: 207. 1869. (Lectotype: *Spruce 1022* NY.)
Murucoa violacea (Aublet) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
Operculina violacea Barb.-Rodr., Vellosia, ed. 2. 1: 60, *tab.* 226. 1891. (Type: *Barbosa-Rodrigues 645* Herb. Mus. Bot. Amaz.-Manaus†?; the plate will be chosen type, if the specimen is proven destroyed.)
O. passifloroides (Meisn.) Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 474. 1932.
Maripa macrosperma Benth. *ex* Roberty, Candollea 14: 43. 1952, *nom. nud. pro syn.*; apparently based on *C. macrospermus* Willd.

Lianas; stems terete, the bark grayish. *Leaves* with petioles 15–35 mm long; blades elliptic, ovate or oblong, 8.5–20 cm long and 4–8.5 cm wide, the base obtuse, the apex shortly acuminate, retuse or obtusely acute, coriaceous to chartaceous, the secondaries 6–10(–13) pairs; glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, 15–30 cm long, ca. 10 cm in diameter, the branches few flowered, often aborting to one; bracts triangular, to ovate, caducous, ciliate. *Flowers* large and showy, with pedicels 8–15 mm long; sepals ovate to widely ovate, 10–16 mm long and 10–15 mm wide, coriaceous, the external lobes glabrous, the internal lobes cano-tomentose with appressed trichomes outside; corolla broad campanulate, violet to dark blue, pale within at base, 35–60 mm long and 30–40 mm wide, the lobes rotund; stamens included, the living filaments white, 17 mm

long, inserted 7 mm above corolla base, the living anthers brown, ovoid, basally sagittate, 8–10 mm long; ovary cylindric to pyriform, 5–6 mm long, ca. 2.5 mm in diameter, glabrous, the living style purple at the base, 35 mm long, glabrous. *Fruits* ellipsoid to ovoid, 30–40 mm long, 20–30 mm in diameter, rugose with a hint of striae, medium to dark brown, the calyx reflexed to ca. 180°; seeds (1–)2–4, trigonous if more than one, otherwise widely ovate, 12–15 mm long, 12–16 mm in diameter.

Lectotype: French Guiana, *Aublet s.n.* P-LAM, not seen; isolectotypes P-DENAIFFE, not seen, BM.

Common names: "Mouroucoa-yarana" (French Guiana—*Aublet*), "murucuarana" or "murucuia-rana" (Brazil—Martius, 1861), "maracujá-rana" (Manaus, Brazil—*Spruce*), "Ooneoballi" (Surinam—*Gonggrijp & Stahel*), "patawana-liane" (Surinam—*Boschbeheer*).

Eastern Guyana, Surinam, French Guiana, and Brazil (Amazonas and Pará); terre firme in wet sandy virgin forest, igapó, swampy secondary forest, capoeiras; flowering April to October; fruiting in April. Illustration: Fl. Bras. 7; *tab.* 73; the dissected corolla is reversed with that of *M. axilliflora* in the same drawing.

BRAZIL. AMAZONAS: Manaus, terra firme, umido, arenoso, mata virgem, fls roxas, trepadeira lenhosa, 23.4.1956, *Coelho & Mello INPA 3766* (INPA). Manaus, Estrada da Raiz, frutex robustus, alte scandens, fls violaceo-cyaneis, 16.4.1936, *Ducke 166* (MO), *166, 2nd* (IAN, MG). Rio Negro, Tapurucoara, igapó, high forest, vine, 13.6.1947, *Froes 22401* (IAN). Along Rio Negro, above Manaus, woody vine, corolla light blue, pale within at base, filaments white, anthers brown, cultivated, 25 m, sandy woods, 14.10.1929, *Killip & Smith 30036* (NY); 7.5.1882, *Schwack 3791* (GOET). Barra (Manaus), forest & capoeiras, stout twiner, anno 185?, *Spruce 1419* (K). Barra, 4.1851, *Spruce 1022* (GH, GOET, K, M, MO, NY, W). PARÁ: km 16 da estrada Castanhal-Marapanim, mata secundaria, pantanoso, cipó, 12.5.1966, *Elias 238* (IAN, MG). Rio Mojú, *Froes s. n., IAN 103744* (IAN).

GUYANA. COURANTYNE: R. B. Mora-mora-bisi Creek, Mapenna Creek, Courantyne River, bush-rope, fls shading to white at center, 24.4.1918, *Hohenkerk C10(713)* (JENM, K).

FRENCH GUIANA. Karouany, anno 1858, *Sagot 1160* (BM, BR, G, K, U, W).

SURINAM. Sectie O, liaan, capoeweri, langs sporosboon, "ooneo'balli," 29.4.1915, *Gonggrijp & Stahel 15* (U). Langs spoorlijn bij km 98, liaan, 29.9.1950, *Lanjouw & Lindeman 3398* (NY, U). Kapoewerie in hoog droogland bos Jodensavanne-Mapangebied bij Suhoza, 4.1960, *Schulz 8265* (U). Zanderij I, 4.1944, *Stahel s. n., U 24196* (U). District of Brokopondo, 10 km NW of village Brokopondo, 30.6.1966, *v. Donselaar 3479* (U). Jodensavanne, Mapanekreek area near km 5 of road, shrubby liane, 2–3 m tall, forest margin, style purple at base, 5.4.1967, *Vreden 11664* (U). Brownsburg, 21.4.1924, *Zaandam (B.W.) 6494* (U); Brownsburg, 23.9.1924, *Zaandam (B.W.) 6644* (A, IAN, U), *(B.W.) 6894*, *(B.W.) 6620* (both U); 4.5.1910, *coll. indig. 173* (U). Pr Tatrich Savanne, 17.4.1910, *coll. indig. 145* (U).

Maripa violacea is not likely to be confused with any other member of the genus. The very large flowers immediately dismiss all other species of *Maripa*, although their general shape might suggest the genus *Ipomoea*. The elliptical leaves, the indehiscent fruits, and the colpate pollen clearly separate the species from *Ipomoea*.

A strong case could be made for separation of *Maripa violacea* into a separate genus as originally published by Aublet (Manitz, 1970). I have chosen not to do this, since the overall aspect of the species immediately suggests *Maripa*. While this species has many very advanced characteristics such as inflorescence and pollen, it also possesses many primitive characters (*e. g.* embryo structure and retention of some endosperm). Total similarity is much like *M. peruviana*, *M.*

nicaraguensis, and *M. panamensis*. These four species must have been derived from a similar ancestor.

Subsection 2. **Melofructae** D. Austin, subsect. nov.

Corollis 25–40 mm longis, inflorescentiis phyllothyrsiformis, trichomatibus dibrachiatis, raro vel nullis stellatis. (Typus *Maripa panamensis* Hemsley.)

12. **Maripa nicaraguensis** Hemsley, Biol. Centr. Amer. Bot. 2: 382. 1882.

Murucoa nicaraguensis (Hemsley) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.
Maripa colombiana Gleason, Bull. Torrey Bot. Club 56: 110. 1929. (Holotype: Colombia, El Cauca, near Salento, *André 2355* K.)
M. cuatrecasasi Moldenke, Phytologia 2: 139. 1946. (Holotype: Colombia, El Valle, at La Trojita, Río Calima, *Cuatrecasas 16531* NY.)

Lianas; stems smooth to slightly angled, grayish-brown to brown. *Leaves* with petioles 10–25 mm long; blades elliptic to lanceolate, 9–15(–25) cm long and 4–6(–11) cm wide, the base obtuse to rounded, the apex acute to shortly acuminate, chartaceous to subcoriaceous, the secondaries in (7–)8–10 pairs; glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, with reddish peltate glandular trichomes on branches; bracts triangular to triangular-ovate, to 2 mm long, mostly persistent in flower, caducous in fruit. *Flowers* with pedicels 4–8(–12) mm long; sepals ovate to broadly ovate, 7–8 mm long and 6–9 mm wide, coriaceous to membranaceous, ciliate, the exterior lobes with reddish glandular trichomes at base, the interior lobes glabrous to appressed pubescent outside; corolla campanulate-funnelform, lilac to pinkish, the tube base nearly white when living, 30–45 mm long, the lobes rotund; stamens included, the filaments 11–12 mm long, inserted 6–7 mm above corolla base, the anthers narrowly ovate, basally sagittate, 6.5–7.5 mm long; ovary cylindric to cylindric-conic, 5 mm long, 1–2 mm in diameter, glabrous, the style (13.5–)20–25 mm long. *Fruits* ellipsoid, broadly ellipsoid to suborbicular, 30–40 mm long, 20–30 mm in diameter, the surface smooth to reticulate, yellow and turning brown to dark brown, the calyx reflexed to 180° or more; seeds (1–)2–4, ovoid, trigonous if more than one, 20–22 mm long, 12–13 mm in diameter.

Holotype: Nicaragua, Chontales, June 1868, *Tate 418* K.

Common names: "Bejuco parra" (Petén, Guatemala—*Aguilar*), "Indian honey" (Middlesex, Belize—*Gentle*).

Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia and Ecuador (Esmeraldas); thickets, rainforests, river side, lake shore to swamps; from sea level to 975 m; flowering January to August; fruiting April to January. Illustration: "Flora of Guatemala," Fieldiana, Bot. 24 (9,1–2): 69–70, *Fig.* 9. 1970.

BELIZE. MIDDLESEX: Stann Creek, high ridge, "Indian honey," 1.6.1939, *Gentle 2809* (NY); high ridge on hill top, 15.7.1939, *Gentle 2913* (A, F, NY). Stann Creek Valley, Antelope Ridge, in mountain cabbage ridge, *Gentle 3183* (A, NY, US). DISTRICT UNKNOWN: Moho River, forest, 16.3.1906, *Peck 717* (GH, K). Tall climber growing in forest shade, 30 feet tall, diameter 4 inches, rare, 200 feet, 10.8.1929, *Schipp S14* (F, GH, NY). Rio Grande River, tall vine growing in forest shade, 60 feet tall, rose coloured fls, occasional, 250 feet, 6.2.1933, *Schipp 1123* (A, BM, F, G, GH, K, MO, NY).

COLOMBIA. ANTIOQUIA: Río del Quindio prope Salento (Quindio), rami flexuosis, ramuli floris erecta, 13.3.1876, *André 2355* (K). BOLIVAR: Vicinity of Estrella, Cano Papayal, lands

of Loba, *Curran 331* (US). San Martín de Loba & vicinity; lands of Loba, *Curran s. n., US 537594* (US). CHOCO: Costa del Pacifico, Bahia de Solano, camino entre Mutis y el Valle, bejuco, frts amarillos, 9.6.1950, *Fernandez 308* (COL, not seen, US). Istmina, on Río San Juan, high climbing woody vine, thickets, ca. 75 m, 29.4.1939, *Killip 35451* (A, COL, not seen, F, US). MAGDALENA: Carare, 7.10.1874, *André 319* (K, NY). META: Sierra de la Macarena, Centr Mts, S. Ridge, dense forest, 900 m, frts, 6.1.1950, *Philipson, Idrobo & Jaramillo 2037* (BM). SANTANDER: Vicinity of Barranca Bermeja, Madgalena River Valley, between Sogamoso & Colorado Rivers, 100–500 m, fls, common in forest, 24.1.1935, *Haught 1542* (COL, not seen, US). EL VALLE: Costa del Pacifico, Río Naya, brazo Ají, orilla derecha en Calle Larga, 1–4 m, 28.2.1943, *Cuatrecasas 14979* (COL, not seen, F). Río Calima (region del Choco), La Trojita, gran bejuco, frt amarillo, 2 semillas envueltas en gelatina parda, oscura, dulzaina, *Cuatrecasas 16531* (COL, not seen, F, NY, photos F, MO, NY).

COSTA RICA. ALAJUELA: Villa Querada, San Carlos, rain forest, Carib watershed, forest shade, soil mold & loam, shrub 3 m, stems fasciculated, buds purple and white tips, 21.2.1939, *Austin-Smith H1616* (F). Villa Querada, forest edge, semi-shade, soil loam, scandent shrub, often with creeping stems, fls on short lateral branches, fls tube base nearly white, 15.3.1939, *Austin-Smith 1784* (F, NY). Vicinity of Los Chiles, Río Frio, frt yellowish, dense forest edge along Río Frio, low tropical rain forest, with palms prominent, 30–40 m, 1.8.1949, *Holm & Iltis 688* (BM, G, U). GUANACASTE: Vicinity of Tilaran, moist forest, large woody vine, *Standley & Valerio 46561* (US). LIMÓN: Jimenes, llanos de Santa Clara, 650 m, 4.1894, *Donnell-Smith 5118* (G, GH, US). Suerre, llanuras de Santa Clara, altitude 300 m, 4.1896, *Donnell-Smith 6656* (G, GH, K, M, US). Finca Montecristo, on Río Reventazon below Cairo, wet forest, buds purple, ca. 25 m, *Standley & Valerio 48529* (F, US). E coast, 17.4.1949, *Stone 1* (F). Río Pacuare, rain forest above Pacuare, fls, 900 m, 7.4.1949, *Williams 16214* (F). PUNTARENAS: Forested hills near Palmar Noof Osa, fls, 75 m, 24.3.1951, *Allen 6025* (GH). Vicinity of Tinoco Station, area between Río Esquinas & Palmar S of Osa, liana climbing 50–60 feet into trees, fls, frequent, 100 feet, 16.3.1950, *Allen 5484* (G, US). Forêts de Santo Domingo de Golfo Dulce, 3.1896, *Tonduz 7088* (US), *9958* (BR). Cerro del Volcan près Boruca, 1200 m, arbre, 3.1892, *Tonduz 6741* (BR). SAN JOSÉ: Basin of El General, fls pink, 675–900 m, *Skutch 4744* (A, F, NY, US). PROVINCE UNKNOWN: Guapiks (Pococi), Finca "La Granja," 100 m, 2.1895, *Tonduz & Pittier 9185* (G, US).

ECUADOR. ESMERALDAS: Borbón, river side, bush, fls violet red, frt violet, 10 m, 25.8.1947, *Harling 1997* (MO).

GUATEMALA. ALTA VERA PAZ: Near Finca Sepacuite, climbing tall trees, fls, 29.4.1902, *Cook & Griggs 784* (US). Near Chirriacte on the Peten hwy, dense wet limestone forest, large vine, ca. 900 m, 9.4.1941, *Standley 91696* (F). Along Río Polochic below Tamahu, rocky, by river, corolla purple, ca. 975 m, *Standley 91770* (F). Pamajche, 150 m, 3.1908, *v. Turkheim 2252* (US). IZABAL: Near Puerto Barrios, Manicaria swamp, sea level, *Standley 76163* (F). Between Virginia & Lago Izabal, Montana del Mico, calyx orchid-lavender, 50–500 m, 5.4.1940, *Steyermark 38835* (F). Río Dulce between Livingston and 6 miles up river, corolla orchid-rose-lavender, 1–25 m, 14.4.1940, *Steyermark 39407* (F). PETÉN: San Diego, Río Pasion, river bank, woody vine, "bejuco parra," 13.4.1935, *Aguilar 436* (F, MO, NY).

HONDURAS. ATLANTIDA: Vicinity of La Ceiba, in thicket along Danto River, foothills of Mt. Cangrejal, frt orange-yellow, 6.8.1938, *Yunger, Koepper & Wagner 8838* (F). PROVINCE UNKNOWN: Shore of Laguna Quemada, 3.3.1903, *Wilson 633* (NY, US).

NICARAGUA. CHONTALES: Vicinity of La Libertad, dense moist mixed forest, ca. 500–700 m, *Standley 9073* (F). Anno 1867–68, *Tate 243-418* (holotype K), *245* (K). RÍO SAN JUAN: Forest along Río San Juan between San Juan del Norte (Greytown) & Delta de San Juan, on branches of tree overhanging river, frts glossy and light green, 0–50 m, 25–25.3.1961, *Bunting & Licht 853* (F). Anno 1961, *Bunting & Licht 708* (F). ZELAYA: Guamil entre El Centro de la Cruz, areas pantanosas a lo largo del Río Grande, fls rosadas, 0–15 m, 26.4.1949, *Molina R. 2446* (F). Along highway between El Recreo e el Pijibaya, rain forest & wet thickets, corolla purple, ca. 40 m, 11.5.1949, *Standley 19889* (F). Pr Bluefields, Mosquito River, anno 1865, *leg. ign. s. n.* (GOET). DEPARTMENT UNKNOWN: *Seemann 86* (BM).

PANAMA. BOCAS DEL TORO: Río Teribe, between Quebrada Tregalo & Puerto Palenque, mostly gallery forest with cloud forest elements, vine, fls purple, 100–116 m, 12.4.1968, *Kirkbride & Duke 526* (MO). CANAL ZONE: 12 miles S of Colón, frts orange-yellow, very hard, 4 large seeds embedded in a black molasses-like gum ca. 1 mm thick, pericarp wall yellow, ca. 3 mm thick, 12.7.1966, *Tyson, Dwyer & Blum 4477* (MO). COCLÉ: El Valle, cloud forest, high climbing liana, frt green, 800–1000 m, 28.6.1967, *Duke 13183* (MO). COLÓN: Santa Rita lumber road, ca. 15 km E of Colón, high vine, fls pale lavender, frts yellow, 9.3.1968,

Dressler 3406 (MO). DARIÉN: Between Quebrada Venado & Peje Swamp on headquarters of Río Tuqueza, vine, frts green, 28.6.1967, *Bristan 1017* (MO). Río Ucurganti, bejuco, frt amarillo, 7.7.1967, *Bristan 1141* (MO). Río Chucunaque, between Río Membrillo & Río Subcuti, vine, frt greenish-yellow, 21.8.1966, *Duke 8608* (MO). Road from El Real to Pinogana, 20.6.1962, *Duke 4898* (MO). Perrecenico River, vine with green frts turning to yellow, *Duke & Bristan 237* (MO). Río Areti, vine, frts, 7.11.1967, *Duke & Nickerson 14913* (MO); 24.5.1966, *Duke 8356* (MO). Vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, vine, frts green turning yellow, wood anomalous, 7.7.1959, *Stern, Chambers, Dwyer & Ebinger 867* (US, MO, GH, G). Cana-Quasi trail, Chepigana, disc lavender, throat white, woody climber, 18.3.1940, *Terry & Terry 1614* (A, F, MO). Marraganti & vicinity, fls pink outside, white inside, 10–200 feet, 3–9.4.1908, *Williams 985* (NY).

While morphologically very similar to *Maripa panamensis*, *Maripa nicaraguensis* is best placed between that species and *M. violacea*. Corolla shape, size, and fruit characters suggest that these species are quite closely related *inter se*.

Maripa nicaraguensis and *M. panamensis* are the only two species of the genus occurring in Panama. They are very similar but may be easily distinguished by leaf texture and venation and by the dried fruits. The mature leaves of *M. nicaraguensis* are invariably chartaceous and reticulate below with prominent veins. *Maripa panamensis* has coriaceous leaves with the veins sunken and obscured in the rugose lower surface. Both species have smooth fruits when immature, but *M. panamensis* produces strongly striate fruits at maturity.

When Peter (1891) was preparing the Convolvulaceae for Engler & Prantl's *Syllabus der Pflanzenfamilien*, he annotated the specimen (GOET) collected on the Mosquito River near Bluefields, Nicaragua, as a new species. Apparently he realized that the plant was *M. nicaraguensis* before publishing, since no mention of his new name has been found in the literature.

13. **Maripa peruviana** v. Ooststr., Recueil Trav. Bot. Néerl. 30: 197. 1933.

M. rivularis Standley *ex* Roberty, Candollea 14: 42. 1952, *nom. nud. pro syn.*

Lianas; stems terete or compressed toward apex, with glandular peltate trichomes. *Leaves* with petioles 6–15 mm long; blades ovate-oblong to oblong, 4–12.5 cm long and 3–8 cm wide, the base acute to obtuse, the apex gently attenuate, obtuse or slightly retuse, chartaceous to subcoriaceous, the secondaries in 8–10 pairs; glabrescent, scattered glandular pubescent below. *Inflorescences* terminal, subumbelliform- to subcorymbose-thyrsiform, glandular pubescent; bracts short triangular, 0.9–1.5(–2) mm long, the apex acute, persistent. *Flowers* with pedicels 4–6(–8) mm long, reddish glandular; sepals oblong to ovate, 6–7 mm long and 4–6 mm wide, glabrous or sparsely covered with glandular trichomes; corolla funnelform to campanulate-funnelform, lilac or violet, 25–36 mm long, the lobes acute to obtuse; stamens included, the filaments 12–15 mm long, inserted ca. 6 mm above corolla base, the anthers oblong to ovoid, the base sagittate, 6 mm long; ovary oblong-cylindric to conic, 4–6 mm long, 2 mm in diameter, glabrous, the style 19–23 mm long. *Fruits* oblong-ellipsoid, to 25 mm long and to 13 mm wide, slightly striate, dark brown, the calyx loosely appressed; seeds 1, ellipsoid, 13.5 mm long, ca. 8 mm in diameter.

Lectotype: Peru, Dept. Loreto, Mischuyacu, near Iquitos, *Klug 914* F; isolectotypes G, NY, US.

Common names: "Mococo-o" Río Zubineta, Peru—*Klug*), "nucnu-huasca" (upper Río Nanay, Peru—Ll. Williams).

Western Brazil, southeastern Colombia, and eastern Peru; mountain forest, terra firme, near rivers, várzea, riverside, open place on beach; 100–450 m; plants may be found in bloom at any time of the year, apparently with a slight peak January to April; fruiting May to July.

BRAZIL. AMAZONAS: Tonantins, margem inundata do Paraná, flor, 28.1.1944, *Ducke 1539* (A, F, IAN, RB, US). Tonantins, fls roseas, 10.11.1927, *Ducke RB 22519* (RB). Near mouth Rio Embira (tributary of Rio Tarauaca), on terra firme, 21.6.1933, *Krukoff 4958* (A, G, NY). Munic São Paulo de Olivença, near Palmares, várzea, fls violet, 11.9–26.10.1939, *Krukoff 8496* (A, BM, BR, F, G, NY, MO).

COLOMBIA. CAQUETA: Florencia, Quebrada del Río Hacha, matorrales, flor rojo violaceo, 400–450 m, 1.4.1940, *Cuatrecasas 8964* (US).

PERU. LORETO: Florida, Río Putumayo, mouth of Río Zubineta, forest, riverside, fls dark red, ca. 180 m, "mococo-o," *Klug 2197* (G, GH, K, NY, US). Mischuyacu, near Iquitos, forest, 100 m, 2.1932, *Klug 2527* (A, F, NY, US). Yanuyacu, E across Amazon from Iquitos, liana on creek bank in várzea forest, frt green, 6.1967, *Robertson & Austin 88* (MO), Gamitanacocha, Río Mazan, on river bank, shrub 9 m high, fls lilac, 100–125 m, 14.1.1935, *Schunke 21* (F, K, NY, US). Palta-Cocha on upper Río Nanay, "nucnu-huasca," 7.1929, *Williams 3199* (syntypes F, G). Nanay, open place on beach, 8 m tall, fls maroon, 100 m, 11.12.1958, *Woytkowski 5153* (MO). SAN MARTÍN: Chazuta, Río Hullaga, mountain forest, fls violet, ca. 260 m 4.1935, *Klug 4066* (BM, F, GH, MO, NY, US).

14. **Maripa panamensis** Hemsley, Biol. Centr. Amer. Bot. 2: 382. 1882.

Murucoa panamensis (Hemsley) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.

Lianas; stems terete, angled, light brown. *Leaves* with petioles 10–25 mm long; blades ovate, elliptic to obovate, 7–15 cm long and 2–10 cm wide, the base cuneate to ± rounded, the apex shortly acuminate to obtuse, coriaceous, the secondaries in 8–10 pairs, with obvious raised, rugose pattern below between secondaries, dull above; glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, covered with reddish glandular trichomes; bracts triangular, caducous, densely covered with peltate glandular trichomes. *Flowers* with pedicels 3–4 mm long; sepals ovate to broadly ovate, 7–8 mm long and 4–7 mm wide, coriaceous, the external lobes with reddish peltate glandular trichomes, the inner with appressed trichomes or glabrous; corolla campanulate-funnelform, violet to pale lilac, 25–30(–37) mm long, the lobes rounded; stamens included, the filaments 10–11 mm long, inserted 5 mm above corolla base, the anthers narrowly ovate, sagittate basally, 6–7 mm long; ovary long-conic to cylindric-conic, 4–5 mm long, 1.5–2 mm in diameter, the apex occasionally sparsely pubescent, glabrescent, the style 15–17 mm long. *Fruits* ellipsoid to broadly ellipsoid, 27–30 mm long, 17–25 mm in diameter, sulcate with 16–22 sulcae when dry, yellow turning light to dark brown, the calyx reflexed to ca. 180°; seeds (1–)2–4, trigonous when more than one, otherwise ellipsoid to ovoid, 15–17 mm long, 9–10 mm in diameter.

Holotype: Panama, Chagres (River), *Fendler* 255 K; isotypes GH, MO, US.

Common name: "Miel quemada" (Colombia—Castaneda, 1961).

Eastern Panama, northern Colombia, and northern Venezuela; rain forest, high forest near stream side, Barro Colorado Island, premontane rain forest, thickets, near lakes; from sea level to 835 m; flowering December to April; fruiting April to September.

COLOMBIA. ANTIOQUIA: In rain forest near Río León approximately 20–30 km upstream & S of the river mouth & approximately 15 km W of Chicgorodo, less than 100 m, common vine on trees above river-bank, corolla lavender, 16.3.1962, *Feddema 1931* (US). Valle del Bajo Magdalena, junto a los senderos que cruzan a Casabe, 120 m, bejuco generalmente rastrero, abundantes flores de color lila o violeta, comun, 4.3.1964, *Uribe 4704* (MO). BOYACA: El Humbo region, 130 miles N of Bogotá, high forest near stream-side, 2500 feet, fls with sweet odor, mauve, 16.4.1933, *Lawrence 759* (A, F, G, MO, RB, US). META: Villavicencio, vigorous, semi-scandent, fls, full exposure, 1600 feet, 3.1948, *Laudeman 5629* (K).

PANAMA. CANAL ZONE: Near mouth of Río Chagres, fls light amparo purple, 15.3.1935, *Allen 890* (G, MO). Barro Colorado Island, Fairchild Point, 9.7.1934, *Aviles 885* (F); liana flat on tree, 22.7.1931, *Bailey & Bailey 640* (GH); 9.6.1931, *Bailey & Bailey 82* (F); on shore, 26.8.1929, *Bangham 411* (A); growing on ground, *Croat 8743* (MO); fruits yellow, turning black, 8.1.1961, *Dwyer 1477* (MO); anno 1929, *Frost 211* (F). Bujio Station, fr, 5.1861, *Hayes 140* (BM, K). Las Cascadas, 4.1925, *Johansen 21* (US). W of Limón Bay, road along Río Piña-Río Media divide, 12.8.1955, *Johnston 1602* (A); Charity Peaks, 3.8.1955, *Johnston 1524* (A, MO). Tortuguilla Point, fls pink, 9.4.1956, *Johnston 1816* (MO). Barro Colorado Island, frequent in forest, fr, 20.8.1927, *Kenover 504* (US). Pipeline Road between mile markers 0 & 11.1, ca. 16 miles N of Gamboa, rain forest, fls pale pink, 10.4.1969, *Lewis et al. 5467* (MO); 4.21.1937, *Lindsay 467* (F). Río Agua Salud, near Frijoles, 6.3.1923, *Piper 5849* (BM, US); buds pale violet, 3.3.1923, *Piper 5796* (US). Agua Clara, on Trinidad River, 10–40 m, 19–21.6.1911, *Pittier 3994* (NY, US). Barro Colorado I, fr white to black when ripe, NE to N shore, 27.8.1929, *Salvoza 876* (A); Fairchild Pt, 9.7.1934, *Shattuck 885* (MO, US); 1.3.1932, *Shattuck 772* (F, MO); wet forest, 18–24.11.1925, *Standley 40979* (US); Wheeler Trail, fr, 7.1931, *Starry 138* (MO). Gamboa, Navy Pipeline Road, 10 miles NE of Gamboa Bridge, vine, fr pale green, 29.5.1957, *Stern & Chambers 20* (MO). Drowned forest between Tumba Vieja & Salamanca, fls white, 66 m, 3.12.1934, *Steyermark & Allen 16756* (M). Fort Sherman, salt marsh, *Tyson 3760* (MO). Road from Fort Sherman to Fort San Lorenzo, fl purple, 16.4.1966, *Tyson & Blum 3760* (MO). Barro Colorado Island, Snyder Molino Trail, liana 100–125 feet high, 24.7.1929, *Wetmore & Woodworth 855-10* (A, F); Allison-Armour Trail at 2200 m mark, 27.7.1929, *Wetmore & Woodworth 880-39* (A, F); Allison-Armour Trail ca. 1300 m mark, fr, 27.7.1929, *Wetmore & Woodworth 886-47* (A, F); Zetek Trail at 1600 m mark, 31.7.1929, *Wetmore & Woodworth 898-59* (A, F); shore, 26.2.1931, fl, *Wilson 63* (F, MO); shore W of Point Salude, 5.2.1932, *Woodworth & Vestal 418* (A, F, M); shore N of end of Chapman Trail, fl light purple, 12.2.1932, *Woodworth & Vestal 503* (F, MO). COLÓN: Vicinity of Piña, 0–50 m, 7.4.1946, *Allen 3428* (BR, F, G, GH, MO, NY, U, US). Road to Piña, fr green, 25.8.1967, *Kirkbride & Hayden 323* (MO). DARIÉN: Camp Esloganti, premontane rain forest, fl pink, 656 feet, 15.3.1968, *Duke 15503* (MO). Cerro Pidiaque, fl lilac, fr green, 5.4.1966, *Duke 8076* (MO). Cerro Pidiaque, fl pink, easily deciduous, 23.4.1966, *Duke 8122, 8123* (both MO). Hydro Camp Pico Pendejo in Monsoon forest on Río Sabana, liana, fl lilac, 50 feet, 15.3.1968, *Duke 15431* (MO). Cocalito near beach, fr brown-black, 8.13.1963, *Dwyer 5135* (MO); vicinity of La Palma, 0–50 m, 1.1912, *Pittier 5489* (GH, NY, US). Vicinity of Cana, in dense woods, fr green, 1750 feet, 24.6.1959, *Stern et al. 510* (G, MO, US). Cerro Piriaque between 100–1000 feet, fl pink, 23.4.1966, *Tyson, Duke & Loftin* 3833 (MO). 3 miles E Santa Fe, fr green, 16.7.1966, *Tyson et al. 4717* (MO). Marraganti, fl pink outside, white inside, 4.4.1908, *Williams 985* (US). PANAMÁ: Along Río Juan Díaz, fl mauvette, ca. 30 m, 28.3.1935, *Allen 935* (G, GH, MO). Hills above Campana, fl purple, 600–800 m, 23.12.1938, *Allen 1695* (MO). Woods along PanAm Highway, ca. halfway between El Llano & Río Mamoni, fr brown, 14–15.9.1962, *Duke 5650* (MO), Cermano, vine in dense woods, 4.1965, *Dwyer & Robyns 104* (MO). Cladonia Harbor, Mt. Vernon, 3.4.1939, *Elmore L13* (GH). Near Arraijan, thickets & forests, ca. 15 m, 21.7.1938, *Woodson et al. 1338* (A, F, MO, NY). SAN BLAS: Along road between Mandinga & Cangandi, fr green, turning brown, 25.10.1967, *Duke 14731* (MO).

VENEZUELA. APURE: Reserva Forestal San Camilo, selva seimpreverde a lo largo de la Quebrada Botina, unos 2 km al suroeste del caserío San Camilo (El Nula), 250 m, 28.3.1968, *Steyermark, Bunting & Blanco 101510* (VEN); corolla lilac on lobes, gray-lilac on lower half, 28.3.1968, *Steyermark, Bunting & Blanco 101504* (VEN). Selva siempre verde de terreno plano, 7 km al este de la Ceiba, 16 km al este de Jordan (viejo), 200 m, 6.4.1968, *Steyermark, Bunting & Blanco 101923* (VEN). A lo largo de la Quebrada de El Dique, al suroeste del caserío San Camilo (El Nula), corolla gray-lavender without & pale lavender on lobes, 250 m, 29.3.1968, *Steyermark, Bunting & Blanco 101540* (VEN). TACHIRA: Veradales, tallos con

franjas estriadas, fr amarillo, bosque humedo tropical, en Potreros, 360 m, 25.4.1964, *Ijjasz-Madriz 325* (VEN). ZULIA: Vicinity of Perija, near Lake Maracaibo, *Tejera 144* (US). Perija, Maracaibo, *Barston s.n.* (W).

15. **Maripa stellulata** Steyermark, Acta Bot. Venez. 3: 209–211. 1968.

Lianas; stems terete, furfuraceo-stellate when young, glabrescent. *Leaves* with petioles 15–22 mm long, densely stellate-pubescent; blades ovate to ovate-oblong, (5–)8–12 cm long, (4–)6–9 cm wide, the base truncate to widely rounded, the apex rounded, often abruptly mucronate, subcoriaceous to coriaceous, the secondaries (6–)8–9(–10) pairs; scattered stellate above, below moderately stellate pubescent, the nerves and laterals heavily pubescent. *Inflorescences* terminal, subumbelliform, 4–10-flowered, the pedicels and peduncles densely stellate pubescent; bracts triangular to ovate, caducous in bud. *Flowers* with pedicels 4–5 mm long; sepals ovate to broadly ovate, 5–6 mm long and 5–8 mm wide, coriaceous, the margins ciliolate, the external lobes moderately to densely stellate pubescent; corolla funnelform, white, 25–30 mm long, the lobes ovate-lanceolate to oblong, the apex obtuse to rounded; stamens included, the filaments 8–9 mm long, inserted 5 mm above corolla base, the anthers oblong, basally sagittate, 5 mm long; ovary conic-oblong, 4 mm long, 2 mm in diameter, glabrous, the style 15–17 mm long, glabrous. *Fruits* unknown.

Holotype: Venezuela, Carabobo, 2.4.1966, *Steyermark & Steyermark 95456* VEN; isotypes MO, U, NY, US.

Northern Venezuela; evergreen mountain forest; 350–1300 m; flowering April to May; fruits unknown; Illustration: Acta Bot. Venez. 3: *Fig.* 25, pg. 210. 1968.

VENEZUELA. ARAQUE: Parque Nacional, near Rancho Grande, ca. 1000 m, dense forest, high-climbing woody vine, corolla pinkish white, 20.5.1943, *Killip & Lasser 37824* (VEN, US). Selvas de la Regresiva del Diablo, Parque Nacional, liana, 1300 m, 15.4.1947, *Pittier & Nakichenovich 15370* (VEN). CARABOBO: A lo largo del Río San Gian, entre arriba de la Planta Electrica y 2 kms debajo de la Planta Electrica, al sur de Borburata, selva siempre verde, 350–550 m, 2.4.1966, *Steyermark & Steyermark 95456* (MO, NY, U, US, VEN).

When I first saw Steyermark's collections of this species in Caracas in 1967, I was fully convinced that it was a new species. Since that time I have examined a large number of specimens from Colombia, Venezuela, and Panama, and I have certain reservations. All specimens I have examined from Panama and Colombia are remarkably constant and do not approach this species. In Venezuela, however, there are specimens clearly referable to *Maripa panamensis*, and others which do not completely conform with that species. These specimens are intermediate between *M. panamensis* and *M. stellulata* but morphologically more similar to the former.

The mountain orogenies in northwestern South America must have played a large part in speciation in various groups. When separations occurred there must have been numerous valleys where populations of *Maripa* were isolated and thus able to evolve independently. This must be true for many taxa found in the Coastal Ranges of Venezuela.

Until more data are known I feel that *Maripa stellulata* is best considered distinct, though closely related to *M. panamensis*.

Subsection 3. **Yacuascae** D. Austin, subsect. nov.

Corollis 10–25 mm longis, inflorescentiis aphyllothyrsiformis, trichomatibus vulgo stellatis. (Typus *Maripa repens* Rusby.)

16. **Maripa repens** Rusby, Descr. South Amer. Pl. 103. 1920.

Lianas; stems with striae, often repent, the repent branches sparsely leafy, the bark white-brown, flaky. *Leaves* with petioles 15–20 mm long; blades narrowly elliptic to ovate, 10–18 cm long and 4–7 cm wide, subcoriaceous to coriaceous, the base attenuate, the apex acuminate, the secondaries in 8–9 pairs. *Inflorescences* axillary, paniculate-thyrsiform to subumbelliform, to 8 cm long and 6–7 cm wide, the lower inflorescences often smaller; bracts ovate, apically acute, ciliate and covered with glandular peltate trichomes. *Flowers* with pedicels 4–7 mm long; sepals ovate to broadly ovate, 4–7 mm long and 4–8 mm wide, subcoriaceous, covered with glandular peltate indument and occasionally some stellate trichomes; corolla funnelform, 20–25 mm long, the lobes rotund; stamens included, the filaments 9 mm long, attached 3 mm above corolla base, the anthers 6 mm long, oblong, basally sagittate; ovary cylindric to ovoid, 3 mm long, 1.5 mm in diameter, the base glabrous, the apex shortly villose, the style 15 mm long. *Fruit* ellipsoid, 40 mm long, 20 mm in diameter, surface slightly striate, dark brown; seeds one, oval-ellipsoid, 20 mm long, 10–12 mm in diameter.

Holotype: Venezuela, Delta Amacuro, lower Orinoco near Saucapana, anno 1896, *Rusby & Squires* NY.

Known only from the lower Orinoco River region in Venezuela; found repent along river margins, and climbing high into trees beside the river; flowering April; initiating fruits in late April.

VENEZUELA. BOLIVAR: La desembocadura de los ríos Nichare y Cicuta (Icuta), affluentes del Río Cuara, 6° 25′ N, 64° 50′ W, 150 m, 24-28.4.1966, *Steyermark & Gibson 95648* (MO, US, VEN). DELTA AMACURO: Saucupana, 4.1896, *Rusby & Squires* 92 (BM, F, G, GH, K, MO, US).

The collection *Rusby & Squires* 92 may prove to be an isotype. This collection has thicker leaves than the type, as does the Steyermark and Gibson collection, but this is perhaps because the type has only immature leaves. It is not at all uncommon for the young leaves of *Maripa* to differ somewhat in texture from mature ones.

This species, *Maripa fasciculata*, and *M. pauciflora* are all closely allied and often difficult to distinguish. The group will be better understood when more collections are available.

17. **Maripa fasciculata** v. Ooststr., Recueil Trav. Bot. Néerl. 30: 195. 1933.

Lianas; stems angular, long striate, gray-brown. *Leaves* with petioles 13–35 mm long; blades elliptic, 10–17 cm long and 5–10 cm wide, the base obtuse to subcordate, the apex obtuse, shortly acuminate, chartaceous to coriaceous, the secondaries 7–11 pairs; glabrescent above, scattered stellate pubescent below, glabrescent. *Inflorescences* axillary, fasciculate-cymose, to 8 cm long, 6–25-flowered, stellate and glandular peltate trichomes covering branches; bracts triangular

to ovate, densely stellate. *Flowers* with pedicels 3–5 mm long; sepals ovate to widely ovate, 4–5 mm long and 4–5 mm wide, the outside lobes ciliate and scattered stellate, the interior lobes glabrous or with central portion sparsely appressed pubescent outside, the margins ciliate; corolla funnelform, white, 15–20 mm long, the lobes rotund, crenulate when dried; stamens included, the filaments 7–8.5 mm long, inserted 5 mm above corolla base, the anthers 3–4 mm long, oblong to narrowly ovate, basally sagittate; ovary cylindric-oblong, 2 mm long, ca. 1 mm in diameter, glabrous, the style ca. 16 mm long, the stigma occasionally shortly exserted. *Fruits* unknown.

Holotype: Peru, Loreto, Mischuyacu, near Iquitos, forest, 100 m, 11–12.1929, *Klug 314* F; isotypes G, NY, US.

Peru and Colombia; forest; 100–700 m; flowering October, November and March; fruits unknown.

COLOMBIA. EL META: Villavicencio, Buenavista, high-climbing woody vine, leaves not seen, corolla pinkish white, 700 m, woods, 18–20.3.1939, *Killip 34511* (US).

18. **Maripa pauciflora** D. Austin, sp. nov.

A *Maripae fasciculatae* similibus, sed pauciflori, nervis lateralibus paucioribus (utrinque 7–9), petiolis minoribus (13–20 mm longis), et foliis coriaceis costis et venis supra valde impressas subter prominentibus differt.

Lianas; stems somewhat angled, striate, gray-brown. *Leaves* with petioles 13–20 mm long; blades elliptic to elliptic-oblong, 11–15 cm long and 5–9 cm wide, coriaceous, the base obtuse to ± rounded, the apex acute, acuminate, or obtuse, the secondaries 7–8(–9) pairs. *Inflorescences* axillary, subracemose to subumbelliform, to 4 cm long, 9–15-flowered, densely yellow stellate on branches and calyx base; bracts triangular, to 1.5 mm long, densely stellate, persistent. *Flowers* with pedicels 2–3 mm long; sepals ovate to widely ovate, 3.5–4 mm long, 4–5 mm wide, glabrous except for glandular and stellate trichomes on the base, ciliate; corolla funnelform, 18 mm long, the lobes obtuse; stamens included, the filaments 6 mm long, inserted 3 mm above corolla base, the anthers 4–4.5 mm long, narrowly ovate, basally sagittate; ovary ovoid, 3 mm long, ca. 1.5 mm in diameter, glabrous, the style 14 mm long, the stigma reaching the corolla lobes. *Fruits* ellipsoid to ellipsoid-globose, 20–25 mm long, 17–19 mm in diameter, striate, light brown, yellow when living, the calyx reflexed to more than 180°; seeds 1–3, ovate-trigonous, 13–14 mm long, 7–8 mm in diameter.

Holotype: Colombia, El Meta, Villavicencio, *Sprague 142* K; isotype US (Fig. 42).

Southeastern Colombia, southern Venezuela, and western Amazonian Brazil; found along river margins and in the forest; 118–130 m; flowering October to March; fruiting May to June.

BRAZIL. AMAZONAS: Tefé, campo de roçado, cipó, fl branca, 13.9.1947, *Black 47-1419* (IAN).

VENEZUELA. AMAZONAS: Bejuco leñoso sobre los arboles en las margenes del Orinoco, Esmeralda, 6.1942, fr 130 m, *Williams 16074* (F, US, VEN). Alto Casiquiare, fr redondo arracimado, amarillo pallido, 28.5.1942, *Williams 15629* (VEN). Capihuara, Casiquiare, 118 m, *Williams s.n.* (F 1192210).

Maripa fasciculata and *M. pauciflora* are similar and must be closely allied. The latter species may be recognized by its fewer-flowered inflorescences, having 9–15 flowers, the 7–9 lateral secondary leaf veins, and the petioles 13–20 mm long. *Maripa fasciculata*, in contrast, has to 25 flowers per inflorescence, to 11 lateral secondary leaf veins, and petioles to 35 mm long. The flower pedicels average 2 mm shorter in *M. pauciflora*; the corollas are mostly shorter, and the deeply impressed leaf veins are characteristic.

19. **Maripa putumayana** D. Austin, sp. nov.

Species affinis subsectio *Yacuascae*, sed speciebus aliis corollae lato campanulatis et bracteis ante anthesin caducis differt.

Lianas; stems flattened to angled, striate, gray. *Leaves* with petioles ca. 25 mm long; blades elliptic 13–15 cm long and 6–8 cm wide, mature foliage leaves not seen but immature leaves chartaceous with veins not prominent below, not sunken above, the base acute, the apex acute to acuminate, the secondaries 7–8 pairs. *Inflorescences* axillary, subumbelliform, ca. 3 cm long, with glandular and stellate indument on branches and calyx base; bracts caducous in flower and not seen. *Flowers* with pedicels 4 mm long; sepals ovate to broadly ovate, 4–5 mm long and 3.5–5 mm wide, the outer with glandular trichomes, the inner with appressed indument along central outside portion; corolla campanulate, 22–23 mm long and 15–25 mm wide, the lobes rotund; stamens included, the filaments 11–12 mm long, inserted ca. 3 mm above corolla base, the anthers 3 mm long, oblong, basally sagittate; ovary cylindric, 3 mm long, ca. 1 mm in diameter glabrous, the style 17–18 mm long. *Fruits* immature, subglobose, smooth, brown, the calyx loosely appressed; seeds unknown.

Holotype: Colombia, Putumayo, Puerto Porvenir, arriba de Puerto Ospina, hacia La Loma, gran bejuco leñoso, fl en umbelas caulinares, blanco-roseadas, selva higrofila del Río Putumayo, 230–250 m, 22.11.1940, *Cuatrecasas 10736* US (Fig. 43).

This Colombian-Ecuadorian species is distinct from all others in the genus. In some ways it approaches *Maripa violacea*, in others the members of subsect. *Yacuascae*. Strong justification could be made for establishing another section of the genus for the species, but to base this on one collection would be foolish.

Vegetative characters suggest a strong alliance with other members of the subsect. *Yacuascae*, but the campanulate corolla is distinctive. The sparcity of material has made it impossible to examine the species palynologically, but when this is done it should be possible to make a better placement of the species in the genus.

2. Dicranostyles

Dicranostyles Benth., London Jour. Bot. 5: 355. 1846.

Kuhlmanniella Barroso, Rodriguesia 9: 36. 1945.

Lianas reaching over 30 m; larger stems smooth to slightly fluted, 15 cm in diameter or larger. *Leaves* alternate, simple; petioles canaliculate; exstipulate;

blades chartaceous, occasionally subcoriaceous, the base attenuate, acute to obtuse, occasionally rounded, cordate or truncate, the margins entire, the apex acuminate, rarely truncate; venation brochidodromus; densely appressed puberulous or erect pubescent to glabrescent. *Inflorescences* axillary, racemose, racemose-thyrsiform, cylindric-thyrsiform, or thyrsiform, usually ± fasciculated in leaf axils or along internodes, the branches usually with appressed dibrachiate pubescence; bracts mostly ovate, persistent, pubescent, occasionally glabrous, the bracteoles squamiform. *Flowers* pentamerous, with valvate-induplicate aestivation; sepals quincuncial, the outer usually ovate, the apex usually acute, the inner mostly broadly ovate to subrotund, the apex usually rounded, the exposed surfaces usually pubescent, the covered surfaces usually glabrous, mostly ciliate; corolla subrotate, or funnelform, white, occasionally pinkish, small (to 5(–8) mm long), lobed almost to base when subrotate, or half corolla length or less when funnel-form, the lobes oblong to oblong-triangular, acute to rotund, the margins involute, inflexed, erect or reflexed at anthesis, pubescent outside, rarely inside; stamens epipetalous, excluded between corolla lobes or inflexed and included at corolla tube apex, the filaments filiform to tapering from a widened or dilate-triangular base, the base free or fused to corolla tube, usually inserted near tube apex, if free pubescent with glandular shaggy hairs or glabrous, if fused to tube glabrous but with a ring or longitudinal rows of glandular hairs, or hairs absent, the anthers dorsifixed, versatile, elliptic-rotund, oblongoid, ovoid or trianguloid, the base sagittate; disc cupuliform, five lobed, probably nectiferous; ovary mostly ovoid to conic-ovoid, occasionally obovoid, glabrous or pubescent, the style entire, divided into two short branches, or completely divided, the stigma two-lobed with the lobes flattened, globose, rotund, cylindric or obpyriform, free or closely appressed. *Fruits* nut-like, ellipsoid to ellipsoid-cylindric, the pericarp thick coriaceous to ligneous, 1(–4) seeded through abortion, the seeds glabrous, ovate to oblong-elliptic, trigonous if more than one per fruit, the seed coat soft, coriaceous, the endosperm scanty or apparently absent, cartilaginous, the cotyledons thin, conduplicate, latiplicate, the base investing.

Type: *Dicranostyles scandens* Benth.

Pollen 3-colpate, prolate to prolate-spheroidal; chromosomes unknown; flowering peaks in March and September to November; seeds possibly used by monkeys, as in *Maripa*.

SYNOPSIS OF INFRAGENERIC TAXA

a. Corolla campanulate or subrotate, lobed ½ its length or more, styles 2, free, or one with two branches (occasionally not visible without dissection), the 2 stigma lobes readily distinguishable, free or closely appressed, complanate to capitate and globose ---------- subgenus 1. *Dicranostyles*

Including: 1. *D. costanensis* Steyermark & D. Austin; 2. *D. scandens* Benth.; 3. *D. ampla var. ampla* Ducke; 3a. *D. ampla* var. *castanea* D. Austin; 3b. *D. ampla* var. *attenuata* D. Austin; 4. *D. solimoesensis* Mennega; 5. *D. densa* Spruce *ex* Meisn.; 6. *D. sericea* Gleason; 7. *D. guianensis* Mennega; 8. *D. longifolia* Ducke; 9. *D. villosus* var. *villosus* Ducke; 9a. *D. villosus* var. *lasiocalyx* Mennega.

aa. Corolla funnelform, lobed ½ its length or less, style 1, entire, the stigma obscurely 2-lobed, the lobes closely appressed to fused, cylindrical, obpyriform to globose ---------- subgenus 2. *Kuhlmanniella*

Including: 10. *D. falconiana* (Barroso) Ducke; 11. *D. holostyla* Ducke; 12. *D. integra* Ducke; 13. *D. mildbraediana* Pilger; 14. *D. laxa* Ducke; 15. *D. globostigma* D. Austin.

Artificial Key to Species

a. Leaves glabrous to glabrescent below.
  b. Inflorescence racemose to subracemose ..... 2. *D. scandens*
  bb. Inflorescence thyrsiform.
    c. Style entire, stigma one with 2 indistinct lobes, corolla funnelform.
      d. Calyx glabrous, calyx and pedicels drying black ..... 10. *D. falconiana*
      dd. Calyx sparsely to densely appressed puberulent, calyx and pedicels not drying black.
        e. Leaves oval, glabrous except for rare scattered trichomes above, style ca. 0.5 mm long, the ovary obpyriform ..... 13. *D. mildbraediana*
        ee. Leaves lanceolate to lanceolate-oblong, glabrous, style ca. 1.2 mm long, the ovary ovoid ..... 11. *D. holostyla*
    cc. Style divided for at least part of its length into two branches, stigmas 2, corolla subrotate.
      f. Style divided less than ⅕ its length from the apex and with the stigma lobes commonly flattened, corolla lobes about the same length as the sympetalous basal portion, stamens introrsely bent at anthesis .. 9. *D. villosus*
      ff. Style divided at least ½ its length from the apex and with the stigma lobes mostly globose and capitate, corolla lobes longer than the sympetalous basal portion, stamens erect at anthesis.
        g. Filaments glabrous, leaves with 7–8 pairs of secondary veins, blades 5–8.5 cm long and 2–3 cm wide ..... 4. *D. solimoesensis*
        gg. Filaments glandular pubescent at base, leaves with 5–13 pairs of secondary veins, blades 4–21 cm long and 1.5–8 cm wide.
          h. Ovary glabrous, plants of the coastal cordillera of Venezuela ..... 1. *D. costanensis*
          hh. Ovary pubescent, at least at apex, plants of the Guiana Plateau margins and the Amazon Basin ..... 3. *D. ampla*
aa. Leaves pubescent below.
  i. Inflorescences in dense globose, cymose clusters ..... 5. *D. densa*
  ii. Inflorescences elongate thyrsiform.
    j. Style entire, stigma one with 2 indistinct lobes, corolla funnelform.
      k. Puberulent with closely appressed trichomes on both inflorescence and leaves, stigma obpyriform ..... 12. *D. integra*
      kk. Pubescent with mostly erect trichomes to about ⅓ mm long on inflorescence and leaves, with some small appressed trichomes on inflorescence, stigmas not obpyriform (not seen in *D. laxa*).
        l. Leaves coriaceous, margins distinctly involute, blades 16–19 cm long and 7–10 cm wide, petiole glabrescent, inflorescences from old growth axil ..... 15. *D. globostigma*
        ll. Leaves membranaceous to chartaceous, margins almost plain, blades 6–11 cm long and 2–4 cm wide, petiole densely pubescent, inflorescence from new growth axil ..... 14. *D. laxa*
    jj. Style divided into short branches which are occasionally not visible without dissection, sigmas with 2 distinct lobes or 2 free stigmas.
      m. Corolla lobes pubescent within (the only species in the Guianas with the leaves pubescent below) ..... 7. *D. guianensis*
      mm. Corolla lobes pubescent on the subinflexed apical region only, otherwise glabrous within.
        n. Secondary veins 8–14 (average 10), the style ca. 0.5 mm long, the 2 stigma lobes capitate and often closely appressed, the filament base glandular pubescent ..... 6. *D. sericea*
        nn. Secondary veins 15–24 (average 20), the style ca. 3 mm long, the 2 stigma lobes ± flattened to capitate, rarely appressed, the filament base glabrous ..... 8. *D. longifolia*

Subg. 1. **Dicranostyles**

1. **Dicranostyles costanensis** Steyermark & D. Austin, Ann. Missouri Bot. Gard. 57: 155. 1970.

Lianas; stems gray-red to reddish-brown, smooth, with white lenticels. *Leaves* with petioles 12–20 mm long; blades oblong, elliptic-oblong to ovate, 4–9(–12) cm long and 3–5 cm wide, the base subrotund to obtuse, the apex acuminate, thinly coriaceous, the secondaries in 8–13 pairs; glabrescent on both sides. *Inflorescences* axillary, aphyllothyrsiform, 4–18 cm long, densely cinnamon-brown pubescent; bracts 1–2 mm long, oblong, acute, pubescent. *Flowers* with pedicels ca. 1 mm long; sepals deltoid-suborbiculate, obtuse, 1.5 mm long and 1.9–2 mm wide, pubescent without, glabrous within, margins ciliolate with non-glandular trichomes; corolla subrotate, white, ca. 5 mm long and ca. 5 mm wide, the tube short, ca. 1.2 mm long and ca. 2 mm wide at summit, ca. 1.5 mm wide at base, glabrous without, the lobes elliptic-oblong, thickened and subinflexed at acute apex, ca. 3.5 mm long, ca. 1.8–1.9 mm wide, pubescent without, glabrous within; stamens excluded, the filaments ca. 3 mm long, inserted ca. 1 mm above corolla base, basally glandular pubescent, the anthers ca. 1 mm long, oblong, basally sagittate; ovary conic-oblong, ca. 1 mm long, ca. 0.5 mm in diameter, glabrous, the styles 2, free for 0.5–1.5 mm, mostly united in basal 0.3–0.7 mm, total length ca. 2 mm, glabrous, the stigmas capitate to ± complanate and irregularly lobed. *Fruits* ellipsoid, 22–25 mm long, 17–19 mm in diameter, striae obscure, somewhat shiny, brown to dark brown, calyx reflexed to ca. 180°; seeds 1, ellipsoid, ca. 15 mm long, ca. 13 mm in diameter.

Holotype: Venezuela, Yaracuy, Cerro La Chapa, selva nublada al norte de Nirgua, on ridge leading to Quebrada de Camburito, 1200–1400 m, 9-10.11.1967, *Steyermark, Bunting & Wessels-Boer 100263* VEN.

Coastal Cordillera in cloud forests at 1200–1500 m, and re-occurring in lowlands of Estado Apure at 250–280 m, Venezuela; flowering March, April and November; fruiting November. Illustration: Steyermark & Austin, Ann. Missouri Bot. Gard. 57: 156, *Fig. 1.* 1970.

VENEZUELA. APURE: Reserva Forestal san Camilo, selva siempreverde a lo largo de la Quebrada La Azuilita, al suroeste del caserío San Camilo (El Nula), 280 m, 30.3.1968, *Steyermark, Bunting & Blanco 101634* (VEN). Reserva San Camilo, a lo largo de la Quebrada de la Cristalina hasta la vega del Cerro La Nulita, 250–280 m, 4.2.1968, *Steyermark, Bunting & Blanco 101732* (VEN). ARAGUA: Selvas de la Mesa, Parque Nacional, liana, 1400 m, *Pittier & Nakichenovich 14447* (VEN). DISTRITO FEDERAL: Cerro Naiguata, laderas pendientes del lado del mar que miran hacia el norte, arriba del pueblo de Naiguata, bosque humedo denso, Lomas de Las Delicias, entre Quebrada de Basenilla y Quebrada Guayoyo, 9–12 km SW de Hacienda Cocuizal, alt 1390–1500 m, 15-19.11.1963, *Steyermark 91953* (MO, VEN).

This species is the only *Dicranostyles* yet known from the northern side of the Venezuelian llanos; all other species are from south of the llanos. There is close resemblance between this species and *D. ampla*, especially with var. *ampla* and var. *castanea*, but due to the difference in range and habitat they are not likely to be confused.

2. **Dicranostyles scandens** Benth., London Jour. Bot. 5: 355. 1846.

Lysiostyles epiphytica Pittier, Bol. Soc. Venez. Ci. Nat. 9: 124. 1944. (Holotype: *Williams 14811* VEN).

Lianas; stems grayish-brown, smooth, with scattered white lenticels, glabrescent. *Leaves* with petioles 5–20 mm long; blades oblong to elliptic, 7–10 cm long and 2–5 cm wide, the base attenuate to cuneate, the apex acuminate, thinly coriaceous, the secondaries 7–10 pairs; glabrescent. *Inflorescences* axillary, racemose to subracemose, 2.5–5 cm long, sparsely flowered, with scattered brown to whitish-brown indumentum; bracts squamiform, ca. 1.5 mm long, acute, brown pubescent. *Flowers* with pedicels ca. 2 mm long; sepals deltoid-suborbicular, obtuse to subacute, ca. 2 mm long and ca. 2 mm wide, scattered brown pubescent outside; corolla subrotate, white, ca. 6 mm long and ca. 6 mm wide, the tube ca. 1–2 mm long, glabrous, the lobes 3–4 mm long, brownish pubescent without; stamens excluded, the filaments ca. 3–4 mm long, inserted ca. 1 mm above corolla base, glandular pubescent at dilate-triangular base, the anthers ca. 0.75–1 mm long, oblong, basally sagittate; ovary conic-oblong to ovoid, ca. 1 mm long, ca. 1 mm in diameter, glabrous, the styles 2, free for half to entire length, ca. 3 mm long, glabrous, the stigmas capitate. *Fruits* unknown.

Lectotype: Brazil, Amazonas, Camanaos (below São Gabriel), *Schomburgk 1010* K; isolectotypes BM, F, G, W.

Northwestern Amazonas, Brazil, and adjacent Venezuela and Colombia; várzea and terra firme; to 127 m; flowering January through March. Illustration: Fl. Bras. 7: *tab. 118, fig. 1.*

Brazil. amazonas: Rio Negro, Povoado Pixuna, beira do rio, cipó, fl branca, perfumada, 5.2.1957, *Cavalcante 509* (IAN, MG). Esperança, margem alagada do Javarí, fl branca, 22.3.1944, *Ducke 141* (G, GH, K, NY). Esperança, ad ostium fluminis Javary, várzea, fluvii Solimoes, Igarape Santo Antonio, frutex scandens, fl albis, 9.2.1942, *Ducke 870* (F, IAN, MG, MO, NY, US). Borba, silva non inundabili, fl albis, *Ducke 1001* (IAN, MG, MO, NY, US). Paraná de Castanheiro, Rio Negro, ad ripas inundatas, fl albis oderatis, 5.3.1936, *Ducke RB 35590* (G, RB, US). Alto Rio Negro, seringal Pixuna, terreno várzea arenosa, fl alba, aromaticas, 5.2.1959, *Rodrigues 811* (INPA, RB). Prope San Gabriel da Cachoeira, ad Rio Negro, 1-8.1852, *Spruce 2306* (G, GH, GOET, K, MO, RB, W).

Venezuela. amazonas: Ad flumina Casiquiari, Vasiva et Pacimoni, anno 1853–54, *Spruce 3323* (BR, G, K, MO, NY). San Carlos, a twiner, frequent throughout alto Rio Negro, *Spruce s. n.* (K). In Vasiva ripis, frutex volubilis, fl albi, 1.1854, *Spruce 2300* (K). Victorino, Río Guainia, bejuco lenoso, con fl de color crema, sobre las ramas de un arbol acuatico, 127 m, 21.3.1942, *Williams 14811* (F, G, US, VEN).

Dicranostyles scandens shows great affinity to *D. costanensis* and *D. ampla*. It is most similar to *D. ampla* var. *attenuata* and may possibly be confused with that variety. *Dicranostyles scandens* is the only species with completely glabrous leaves, attenuate leaf bases, and a racemose inflorescence. The lower branches of the inflorescences occasionally bear two or three flowers, but otherwise the racemose situation appears normal.

Normally the ovary of *D. scandens* is glabrous; however, in *Ducke 1001*, the ovary is densely pubescent. This character is normally constant within the family and often used to distinguish species. The collection made by Ducke in Borba is the easternmost plant that has been collected, and the leaf texture differs slightly from the other collections.

3. **Dicranostyles ampla** Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 590. 1932.

D. boliviensis Ducke, Arq. Serv. Florest. 1: 37. 1939. (Holotype *Kuhlmann RB 22-194* RB; isotypes B†, G, IAN, US.)

D. boliviana Mennega, Proc. Kon. Ned. Akad. Wetensch., Ser. C. 71: 551. 1968, *sphalma*.

Lianas; stems brown to reddish-brown, glabrescent. *Leaves* with petioles 5–20 mm long, glabrous; blades oblong, elliptic-oblong, ovate or obovate, 6–21 cm long and 1.5–8 cm wide, the base attenuate, obtuse or rounded to subcordate, the apex acuminate, subcoriaceous, the secondaries 5–11 pairs; glabrescent. *Inflorescences* axillary or clustered at the tip of a lateral branch, cylindric-thyrsiform to pyramidal-thyrsiform, 3.5–19 cm long, pubescent with a hazel to chestnut indumentum. *Flowers* with pedicels ca. 1–2 mm long; sepals ovate to broadly ovate, the outer lobes acute, the inner rounded, ca. 1.5 mm long and ca. 1–1.5 mm wide, appressed puberulent; corolla subrotate, white, 3–4 mm long, the tube ca. 1 mm long, the lobes ca. 2–3 mm long, glabrous inside, the lobes pubescent outside; stamens excluded between corolla lobes, the filaments ca. 3 mm long, inserted ca. 1 mm above corolla base, the base glandular pubescent, the anthers ca. 0.5–0.75 mm long, oblong; ovary ovoid, ca. 1–1.3 mm long, ca. 0.8–1 mm in diameter, the upper half or only the apex pubescent, the styles 2, ca. 2–2.5 mm long, the stigmas globose and capitate to somewhat irregularly lobed around margins. *Fruits* ellipsoid to obpyriform, ca. 15–20 mm long, ca. 12–15 mm in diameter, the pericarp thin, ligneous, almost smooth to striate, dark brown to black; seeds 1, ellipsoid, to ca. 15 mm long, to ca. 10 mm in diameter.

KEY TO VARIETIES OF *DICRANOSTYLES AMPLA*

a. Leaf base attenuate, fruits obovoid to obpyriform ..... 3c. *D. ampla* var. *attenuata*
aa. Leaf base obtuse to subcordate, fruits ellipsoid.
  b. Inflorescences 11–19 cm long, if some shorter, then most within this range, pubescence hazel-brownish, leaves (6–)8–17(–21) cm long and (1.5–)3–6(–8) cm wide ..... 3a. *D. ampla* var. *ampla*
  bb. Inflorescences 3.5–10 cm long, if some longer, then most within this range, pubescence dark chestnut, leaves 7–13 cm long and (2.0–)3.5–5 cm wide ..... 3b. *D. ampla* var. *castanea*

3a. **Dicranostyles ampla** var. **ampla**

Lianas; stems brownish, scattered tomentellous when young. *Leaves* with petioles 5–20 mm long; blades elliptic-oblong to oblong, rarely ovate (6–)8–17(–21) cm long and (1.5–)3–6(–8) cm wide, the base obtuse to subcordate, the apex acuminate, the secondaries in 7–9 pairs; glabrescent. *Inflorescences* axillary and clustered at the apex of a lateral branch, pyramidal-thyrsiform, (4.5–)11–19 cm long, the lower peduncles mostly 10–15 mm long to first flowers, mostly more than three-flowered, brownish puberulent, lenticels commonly visible on inflorescence rachis. *Flowers* with pedicels 1–2 mm long; sepals ca. 1.5 mm long and ca. 1.5 mm wide, brownish puberulent; corolla subrotate, white, ca. 3–4 mm long, the lobes sublinear; stamens excluded between corolla lobes, the filaments ca. 3 mm long, the anthers ca. 0.5–0.75 mm long, oblong; ovary ca. 0.75–1 mm long, ca. 0.5–1 mm in diameter, pubescent at apex only or down sides from apex, the styles ca. 2.5 mm long. *Fruits* (known only from Venezuelan specimens) ellipsoid, to 20 mm long, to 12–15 mm in diameter, dark brown to almost black when dried; seeds 1, ellipsoid.

Holotype: Brazil, Rondonia, ad stationem Presidente Marquez viae ferreae Madeira-Mamoré, frutex ramis flagelliformibus, fl albis, 12.10.1923, *Kuhlmann RB 22492* RB; isotypes G, IAN, K, US.

Bolivar and Delta Amacuro, Venezuela, Bartica, Guyana, and western Amazonia, Brazil; terra firme, bosque pluvial, high forest; flowering October through December; fruiting February and July; 100–320 m in Venezuela.

BRAZIL. AMAZONAS: Içana, Cabary, liana, fl branco palido, forte perfume, 2.12.1945, *Froes 21462* (F, IAN, K, MO, NY, US). Munic. São Paulo de Olivença, basin of cr Belém, vine, terra firme, high forest, 26.10–11.12.1936, *Krukoff 8831* (BM, BR, G, MO, NY, US).

GUYANA. Bartica, 11.1888, *Jenman 4730* (JENM, K, NY).

VENEZUELA. BOLIVAR: Forest at base of Altiplanicie de Nuria, between Rancho Alegre & base of Altiplanicie, on trail to Quebrada Cabeza Burro, 5 km E of Las Chicharras, 47 km N of Tumeremo, 100–250 m, 12.2.1961, *Steyermark 89345* (F, MO, NY, VEN), 899337 (NY, US, VEN). Altiplanicie de Nuria, ± level forest on trail between El Cruzero & slightly beyond pica 101, ENE of Villa Lola, liana, 315 m, 15.7.1960, *Steyermark 86368* (VEN). DELTA AMACURO: Bosque pluvial E de Río Grande, 38 km ENE de El Palmar, cerca de los limites del estado Bolívar, Cerro Moca Hierro, 320 m, 8.2.1964, *Steyermark 93080* (MO, VEN).

3b. **Dicranostyles ampla** var. **castanea** D. Austin, var. nov.

A var. *ampla* similis sed inflorescentibus brevioribus, foliis minoribus et praecipue oblongis, indumentis thyrsis densis cataneis differt. A var. *attenuata* basis foliis obtusis vel subcordatis et fructis ellipsoidis valde differt.

Lianas; stems reddish-brown, glabrescent. *Leaves* with petioles ca. 20 mm long; blades mostly oblong to oblong-elliptic, 7–13 cm long and (2–)3.5–5 cm wide, the base obtuse to rounded, the apex acuminate, the secondaries 9–11 pairs; glabrescent. *Inflorescences* axillary and clustered at the apex of a lateral branch, pyramidal-thyrsiform, 3.5–10(–16) cm long, the lower peduncles mostly ca. 10 mm long to the first flowers, mostly more than 3-flowered, with a dense castanaceous appressed indument, lenticels rarely visible on rachi. *Flowers* with pedicels ca. 1 mm long; sepals ca. 1–1.5 mm long and ca. 1–1.5 mm wide, with the same indument as the inflorescence; corolla subrotate, white, ca. 4 mm long, the lobes sublinear to ± ovate; stamens excluded between corolla lobes, the filaments ca. 3 mm long, the anthers ca. 0.75 mm long, oblong; ovary ca. 1 mm long, ca. 0.5 mm in diameter, glabrous, the styles ca. 3.5 mm long. *Fruits* ellipsoid, to ca. 20 mm long, ca. 12–15 mm in diameter, black when dried, striate; seeds 1, ellipsoid.

Holotype: Brazil, Pará, Belém, Mocambo, 19.12.1950, fl, *Pires 2586* NY; isotypes IAN, INPA, US.

BRAZIL. PARÁ: Belém, S forests of IAN, liana, fr deep purple, almost black, 2.1.1943, *Archer 8118* (IAN). Belém, S forest of IAN, *Archer 7881* (F, G, GH, IAN, K, MO). Belém, Mocambo Reserve on IAN grounds, terra firme near igapó, Q.20–32, liana climbing tree with *Maripa glabra*, old fruits, 20.5.1969, *Austin 4039* (IAN, MO). Igarape Itaramá na estrada para Marapanim, cipó ca. 20 m, ca. 30 cm in diameter near base, flattened, on bank of igarape in sandy soil, old fr, 18.6.1969, *Austin 4207* (MG, MO). Beira do Rio Jamundá, acima de São Jorge, Munic. de Faro, várzea, botão rufo, sem latex, 12.11.1950, *Black & Ledoux 50-10739* (IAN). Rio Jamundá, abaixo da 1ª cachoeira, beira, fls, 17.5.1911, *Ducke MG 11757* (RB 22520) (RB). Gurupá, mata de terra firme, fr preto, 16.5.1916, *Ducke RB 18004* (RB). Belém, Mocambo, IAN, terra firme, fl amareladas, 27.11.1950, *Pires 2685* (IAN, NY). Belém, Mocambo, 19.11.1950, *Pires 2586* (IAN, INPA, NY, US). Mata da Cia. Pirelli, Frazenda Uriboca, terra firme, arvore pequena ou arbusto, com aparência de vara, fl perfumadas, 7.1958, *Pires 6958* (IAN). Belém, Várzea do Aurá, 20 m, cipó, fl marron, sobre arvore de 20 m,

19.10.1967, *Pires & Silva 11303* (IAN). Belém, Reserva Mocambo, cipó, flor marron, sobre arvore de 20 m, 9.1.1968, *Pires & Silva 11349* (IAN). MATTO GROSSO: Royal Society/Royal Geographic Society Expedition 1967/1969, 12°49′ S, 51°46′ W, 26.10.1968, *Harley 10837* (FAU, K, U).

GUYANA. Northern slope of Akarai Mountains, in drainage of Shodikar Creek (Essequibo tributary), dense forest, 300–600 m, liana, fls white, 10–20.1.1938, *Smith 2915* (F, G, MO, NY, US). Basin of Essequibo River, near mouth of Onoro Creek, dense forest, petals brown without, white within, filaments white, anthers pale yellow, 15–24.12.1937, *Smith 2733* (A, F, G, MO, NY, US).

3c. **Dicranostyles ampla** var. **attenuata** D. Austin, var. nov.

A var. *castanea* similis sed inflorescentibus brevioribus, paucifloribus, indumentis avellaneis, foliis basis attenuatis (non obtusis vel subcordatis ut in var. *ampla* et var. *castanea*), et fructis obovatis vel obpyriformibus distinct est.

Lianas; stems grayish-brown to reddish-brown, glabrescent. *Leaves* with petioles 12–22 mm long; blades obovate to elliptic, 4–12 cm long and 1.5–5.5 cm wide, the base attenuate, the apex acuminate, the secondaries 9–11 pairs; glabrescent. *Inflorescences* axillary on short lateral branches, cylindric-thyrsiform, 2.5–6 cm long, the lower peduncles mostly 8–10 mm long to the first flowers, mostly three-flowered or less, with hazel to yellowish-hazel appressed indument, lenticels rarely visible on rachi. *Flowers* with pedicels ca. 1 mm long; sepals ca. 1.5 mm long and ca. 1.5 mm wide, with the same indument as the inflorescence; the corolla and androecium not seen; ovary ca. 1 mm long, ca. 1 mm in diameter, glabrous, the styles not seen. [The measurements of the ovary were taken from flowers in which the styles, androecium and corolla had fallen and may be slightly larger than at anthesis.] *Fruits* obovate to obpyriform, to ca. 25 mm long, ca. 14–15 mm in diameter, dark brown when dried, striae present but barely visible; seeds 1, ellipsoid.

Holotype: Brazil, Acre, near mouth of Rio Macuahan, tributary of Rio Yaco, vine on high tree, fr, 1.9.1933, *Krukoff 5728* MO; isotypes G, NY, US.

BRAZIL. ACRE: Near mouth of Rio Macuahan, tributary of Rio Yaco, vine on high terra firme, buds deformed by galls, 5.8.1933, *Krukoff 5301* (A, G, MO, NY, US); vine on high tree, 1.9.1933, fr, *Krukoff 5728* (G, MO, NY, US). AMAZONAS: Munic. São Paulo de Olivença, basin of cr Belém, vine, terra firme, high forest, 26.10–11.12.1936, *Krukoff 8790* (A, BR, G, MO, NY, US). Ilha do Marapata, boca do Rio Negro, igapó, fr verdes, 20.6.1961, *Rodrigues & Coelho 2831* (MG). RONDONIA: Near Tabajará, upper Machado River region, woody vine on várzea land, along river shore, 11–12.1931, *Krukoff 1464* (A, BM, G, K, MO, NY).

The specimen collected by Kuhlmann (*Kuhlmann RB 22494*) combines the characters of var. *attenuata* and var. *ampla*; it has the inflorescence of var. *attenuata*, but the leaf base and pubescent ovary of var. *ampla*. On first appearance it seems to be intermediate between var. *attenuata* and var. *castanea*, but the pubescent ovary denies this. Ducke named this collection *D. boliviensis*, but I have seen no other collection annotated by him with this name.

Dicranostyles ampla is variable and yet easily divided into three groups. Two of these groups, var. *attenuata* and var. *castanea*, might well be recognized as subspecies, but I suspect their disjunct range is only a reflection of the areas collected. The two varieties *ampla* and *castanea* are morphologically similar and must be quite closely related. Variety *attenuata* is considerably different from them and appears more like *D. scandens*.

The few collections from Venezuela and Guyana do not match the western Amazon Basin collections of var. *ampla* as closely as they should. The specimens from the Sierra Imataca, Venezuela, match much better than does the collection from Bartica, Guyana. While the leaf shape, size and indument on all these collections agree with the Brazilian collections, the inflorescence of the Guyana collection is much more reduced than any other collection of this variety. Since there are insufficient collections to fully understand the variation of this variety, I have not established a new name for these northern collections.

4. **Dicranostyles solimoesensis** A. Mennega, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 71: 555–556, *pl. I, fig. 3*; *pl. IV*. 1968.

Lianas; stems grayish-brown, tomentellous when young, glabrescent. *Leaves* with petioles 6–8 mm long; blades elliptic to obovate, 5–8.5 cm long and 2–3 cm wide, the base attenuate to rotund, the apex narrow, obtuse, shortly acuminate, chartaceous to subcoriaceous, the secondaries 7–8 pairs; glabrescent above and below. *Inflorescences* axillary, probably racemose or cylindric-thyrsiform (*fide* Mennega); bracts 1 mm long, deltoid, reddish-brown pubescent. *Flowers* with pedicels 1 mm long; sepals ovate, acute, 2.5 mm long and ca. 2.5 mm wide, the outside reddish pubescent; corolla subrotate, ca. 5 mm long, the lobes 4.5 mm long, reddish pubescent outside; stamens included between corolla lobes (*fide* Mennega), the filaments 3 mm long, basally dilate, glabrous, inserted at corolla tube apex, the anthers ca. 0.5 mm long, ellipsoid; ovary ovoid, 2 mm long, 1 mm in diameter, tomentose, the style 1 mm long, bipartite almost to base, glabrous. *Fruits* unknown.

Holotype: Brazil, Amazonas, Rio Solimoes, basin of cr Belém near São Paulo de Olivença, *Krukoff 8793* U; isotype MO.

Known only from type collection near São Paulo de Olivença; terra firme in high forest; flowering October to December. Illustrations: Proc. Kon. Ned. Akad. Wetensch., Sec. C. 71: 553, *pl. I, fig. 3*; *pl. IV*. 1968.

The flower structure of this species suggests very close relations with *Dicranostyles scandens*, *D. ampla*, and *D. costanensis*. The leaves, as in these three species, are glabrous, but considerably smaller and of different shape and texture. This is the only species with small leaves, branched styles, and glabrous filaments. By these characters it is readily distinguished from all other species.

5. **Dicranostyles densa** Spruce *ex* Meisner *in* Mart., Fl. Bras. 7: 328. 1869.

Lianas; stems whitish- to yellowish-gray, smooth, with white lenticels. *Leaves* with petioles 10–20 mm long; blades oblong to elliptic-oblong, 13–25 cm long and 4–9.5 cm wide, the base obtuse, the apex acuminate, thinly coriaceous, the secondaries (10–)12–15(–17) pairs; glabrescent above, yellowish pubescent below. *Inflorescences* axillary or along internodes, in dense cymose clusters, densely yellowish pubescent; bracts triangular to ovate-triangular, ca. 1.3 mm long, yellowish pubescent. *Flowers* with pedicels ca. 2 mm long; sepals ovate, acute, 3–3.5 mm long and 1–1.5 mm wide, densely pubescent; corolla campanulate, white to brownish, 5–8 mm long and ca. 8 mm wide, the densely villose lobes

folded introrsely at anthesis, the tips acuminate; stamens included, the filaments bent introrsely, ca. 4 mm long, inserted ca. 2 mm above corolla base, the anthers ca. 1 mm long, oblongoid to trianguloid, basally sagittate; ovary ovoid, ca. 1.5 mm long, ca. 1 mm in diameter, the base glabrous, the upper half densely villose with a long beard which is longer than the glabrous base, the style ca. 3 mm long, glabrous to woolly on upper part, branched at the apex into two arms ca. 0.5 mm long. *Fruits* ellipsoid, 20–22 mm long, 12–15 mm in diameter, with pronounced striae, shiny, black, calyx reflexed to ca. 180°; seeds 1, ellipsoid to ovoid, to 15 mm long and to 10 mm in diameter.

Lectotype: Brazil, Amazonas, Barra (Manaus), *Spruce 1687* K; isolectotypes BR, MO, NY.

Rio Negro and Cassaquire River basins in Amazonas, Brazil and Venezuela; capoeiras on terra firme; flowering April and August to October; fruiting November to April. Illustration: Fl. Bras. 7: *t. 118 II* (Meisner thought that he was using unopened buds for his illustration; however, it appears that the flowers never open much wider than shown in his plate).

BRAZIL. AMAZONAS: Manaus, Igarape do Franco, *Chagas INPA 5723* (INPA). Manaus, Igarape do Leão, terra firme arenoso, fls castanhas, *Coelho INPA 5796* (INPA). Manaus, Frances Novo, *Coelho & Chagas INPA 4221* (INPA, RB). Manaus RB-17 km 3, *Coelho & Mello INPA 3162* (INPA, RB); Manaus, estrada do Igarape da Tabatinga, *Rodrigues & Chagas 2824* (INPA). Cachoeira Grande, silva secundaria non inundabili, fls albidis, 16.10. 1941, *Ducke 808* (F, IAN, MG, MO, NY, US). Manaus, Cachoeirinha, silva secundaria non inundabili, fr maturis nigris, 7.1.1943, *Ducke 1162* (IAN, MG, MO, NY, US). Manaus, locis arenosis prope flumen Taraum superius, fls brunneis, 14.9.1929, *Ducke RB 22571* (RB, U, US). Manaus, Estrada da Raiz, in relictis silvae, fr maturis nigris foetidis, 16.4.1936, *Ducke RB 35588* (G, K, RB, U, US). Manaus, Igarape do Buião, solo agriloso, capoeira, frs verdes, 18.1.1962, *Rodrigues & Coelho 3298* (MG). *Rodrigues & Chagas 4099* (INPA); Manaus, estrada da Forquilha, *Rodrigues & Chagas 4953* (INPA). Barra (Manaus), fr black, polished, capoeira, 3.1851, *Spruce 1762* (K).

Dicranostyles densa is uniquely characterized by inflorescences in dense, cymose clusters which are found mostly along the internodes, flowers larger than other species and curiously campanulate, almost urceolate. The stamens of this species are introrsely bent as in *D. villosus*, but the species are not likely to be confused.

6. **Dicranostyles sericea** Gleason, Amer. Jour. Bot. 19: 751. 1932.

Lianas; stems grayish- to reddish-brown, glabrescent. *Leaves* with petioles 15–20 mm long, appressed pubescent; blades oblong-elliptic to oblong, 11–14 cm long and 5–6 cm wide, the base acute to broadly acute, the apex acuminate, chartaceous, the secondaries 10–13 pairs; glabrate above, red-pubescent below. *Inflorescences* axillary, racemose or narrowly cylindric-thyrsiform, solitary or fasciculate, red- to reddish-white pubescent; bracts ovate, ca. 1 mm long, red pubescent. *Flowers* with pedicels 1–1.5 mm long; sepals ovate to widely ovate, apex rounded, obtuse or shortly apiculate, 1–1.5 mm long and 1–1.5 mm wide, densely red pubescent on exposed surfaces; corolla subrotate, white, 4–5 mm long, the lobes erect at anthesis, the outside pubescent; stamens excluded between corolla lobes, the filaments ca. 2 mm long, inserted at apex of corolla tube, basally glandular pubescent, the anthers ca. 1 mm long, trianguloid; ovary

ovoid, ca. 1.5 mm long, ca. 1 mm in diameter, glabrous, the style ca. 0.5 mm long, glabrous, the two stigmas globose, closely appressed to slightly fused at apex. *Fruits* unknown.

Holotype: Peru, Loreto, Mischuyacu, near Iquitos, *Klug 1132* NY; isotype US.

Known only from three localities in Loreto, Peru; forest; 100–220 m; flowering from February to April. Illustration: v. Ooststr., Recueil Trav. Bot. Néerl. 30: 194, *fig. 1, I.* 1933.

PERU. LORETO: Balsapuerto, ca. 220 m, forest, 3.1933, *Klug 2962* (A, BM, F, G, GH, MO, NY, US). Mischuyacu, near Iquitos, 100 m, 4.1930, *Klug 1156* (US). Gamitanacocha, Río Mazán, 100–125 m, 25.2.1935, *Schunke 318* (A, NY).

The general aspect of this species suggests *Dicranostyles mildbraediana*, with which it might be confused. Yet *D. sericea* is readily distinguished by the subracemose inflorescences and the pubescent leaves; corolla, ovary, and stigma shape also differ greatly. *Dicranostyles integra* could possibly be confused with *D. sericea*, but the thyrsiform inflorescences and funnelform corollas of the former readily separate them.

7. **Dicranostyles guianensis** A. Mennega, Kon. Ned. Akad. Wetensch. Ser. C. 71: 554–555. 1968.

D. imatacensis Steyermark, Acta Bot. Venez. 3: 190–192. 1969. (Holotype *Steyermark 87129* NY, isotype VEN.)

Lianas; stems ferrugineus with small appressed indument when young, glabrescent. *Leaves* with petioles 10–17 mm long; blades elliptic-ovate to broadly ovate, 6–11 cm long, 3–7 cm wide, the base rotund to subobtuse, the apex abruptly acuminate, chartaceous to subcoriaceous, the secondaries 7–12 pairs; glabrate above except along the costa, white to reddish sericeous below. *Inflorescences* axillary and scattered along internodes of short lateral, leafy branches, cymose, commonly 10–15 flowered, ca. 10–20 mm long and wide, occasionally racemose at base, reddish pubescent; bracts 1–2 mm long, ovate, densely red pubescent. *Flowers* with pedicels 2–3 mm long; sepals broadly ovate to ± deltoid, ca. 3.5 mm long and 2.5–3 mm wide, the apex acute, red pubescent; corolla subrotate, deeply lobed, 4–5.5 mm long, the lobes spreading at anthesis, pubescent outside and the lobes pubescent inside; stamens excluded between corolla lobes, the filaments 2–4 mm long, inserted at the corolla tube apex, glabrous, the anthers ca. 1 mm long, narrowly oblongoid; ovary conic, ca. 2–2.5 mm long, ca. 1–1.5 mm in diameter, villose, the style 2–3 mm long, very shortly lobed at the apex, pubescent for ± the lower half, the stigmas 2, complanate and recurved to ± rounded. *Fruits* ovoid, ca. 12 mm long, ca. 9 mm in diameter (probably immature size), grayish, the calyx reflexed to ca. 180°; seeds not seen.

Holotype: French Guiana, Maroni, anno 1864, *Melinon* P.

French Guiana, Surinam, and the Sierra Imataca in eastern Venezuela; flowering October. Illustrations: Menega, *Pl. I, Fig. 1, Pl. III*; Steyermark, Acta Bot. Venez. 3: 190–192, *Fig. 14.* 1969.

French Guiana. *Melinon s. n.* (P).
Surinam. Brokopondo district, sterile, *van Donselaar 2457* (U).
Venezuela. delta amacuro: San Victor, Río Amacuro, Sierra Imataca, 65–80 m, 31.10.1960, *Steyermark 87129* (NY, VEN).

This species and *Dicranostyles longifolia*, as Mennega (1968) has pointed out, are closely related. *Dicranostyles guianensis* is the only species in the genus with the corolla lobes pubescent within.

Mennega, while determining some collections made during the 1800's in French Guiana by Melinon, found specimens which did not fit described species. Unknown to her, Steyermark had collected plants on the Sierra Imataca of Venezuela which he realized were undescribed. After Steyermark's manuscript had been in press for three years, his new species was published and distributed at almost the same time Mennega's appeared. Although the collections on which these two names are based differ slightly in size, there is no doubt that they are the same species since, among other similarities, they both exhibit the unique corollas which are pubescent within.

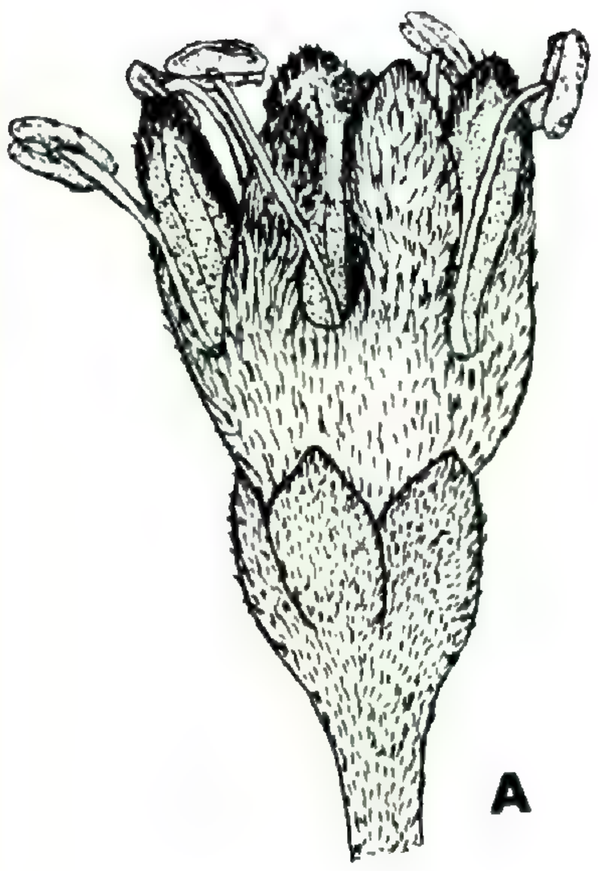
While there is no doubt that Steyermark was the first to realize that this species had not been described, the name proposed by Mennega must be chosen. Steyermark (personal communication, 4.4.1969) said that he "received a personal copy of this volume in late February and other copies were distributed at about this time to the various contributors of the volume." Mennega (personal communication) has informed me that the volume in which her new species occurred was distributed on 17 December 1968. The dock strike in New York undoubtedly delayed delivery of both these volumes, but the publication with Mennega's species arrived at the Missouri Botanical Garden several weeks before the Venezuelan publication. Steyermark (personal communication) wrote that the New York Botanical Garden received their copy of Mennega's publication on 15 March 1969.

8. **Dicranostyles longifolia** Ducke, Arq. Inst. Biol. Veg. 2: 69. 1935.

Lianas; stems whitish to reddish, flattened to four-angled. *Leaves* with petioles 10–20 mm long; blades long lanceolate-oblong, rarely elliptic or ovate, 8–22 cm long and 3–7 cm wide, the base obtuse to subacute, rarely rounded to subcordate, the apex long acuminate to truncate, mucronate, the secondaries 15–24 pairs, chartaceous to subcoriaceous; glabrescent above, with appressed red indument below. *Inflorescences* axillary, cylindric-thyrsiform, to ca. 20 cm long, solitary to fasciculate, occasionally racemose at base, red pubescent; bracts ovate, to 2 mm long, red pubescent. *Flowers* with pedicels 0.5–1 mm long; sepals ovate to ovate-triangular, ca. 2.2 mm long and ca. 1–2 mm wide, the outer lobes with a villose acute tip, inner and outer lobes pubescent outside; corolla subrotate, deeply lobed, white to rosy, 4–5(–6, *fide* Ducke) mm long,

→

Figure 38. Flower structure of *Dicranostyles*.—A–D. *D. longifolia*.—A. Flower.—B. Dissected corolla.—C. Gynoecium.—D. Apical detail of stigma.—E–L. *D. globostigma*.—E. Stigma detail.—F. Gynoecium.—G. Trichome from ovary.—H. External sepal.—I. Internal sepal.—J. Anther, interior view.—K. Anther, exterior view.—L. Dissected corolla.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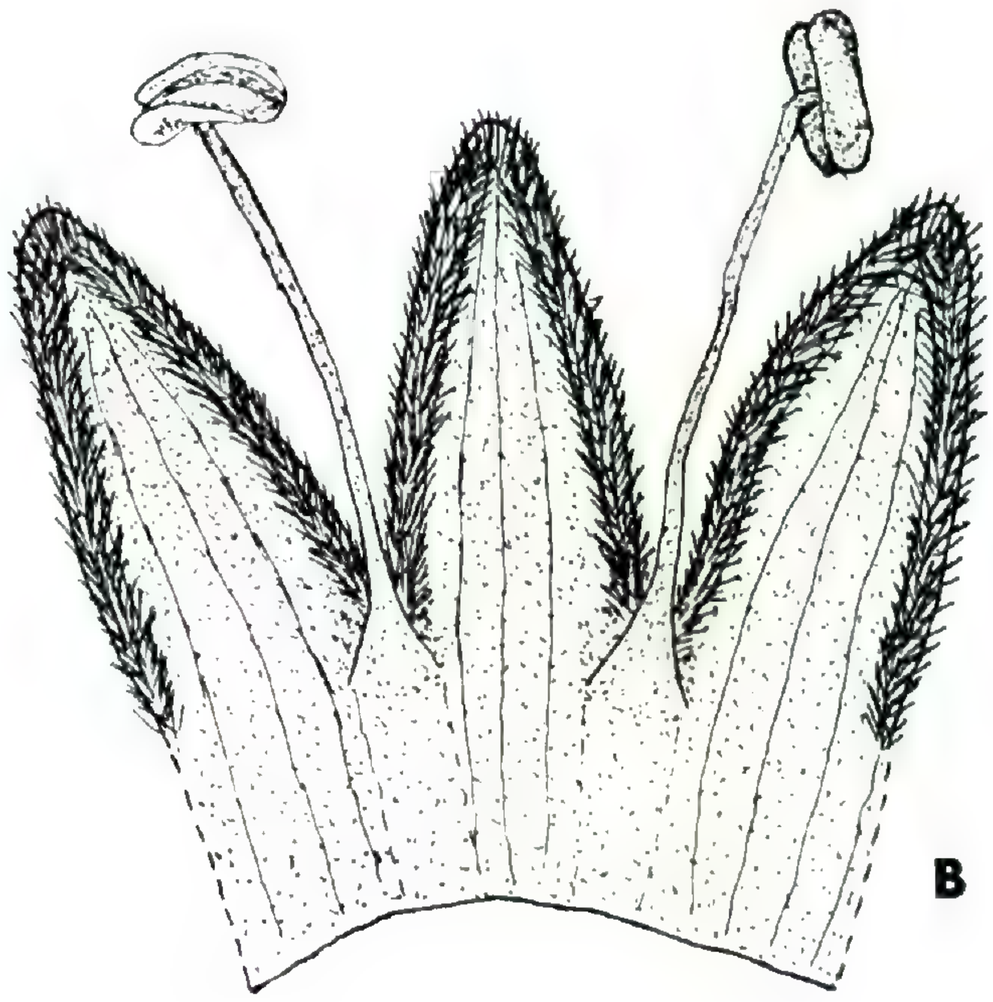
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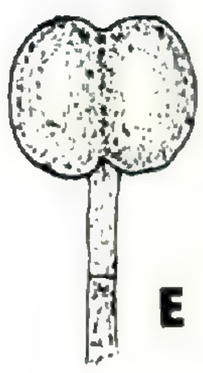
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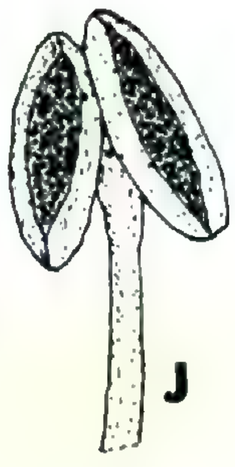
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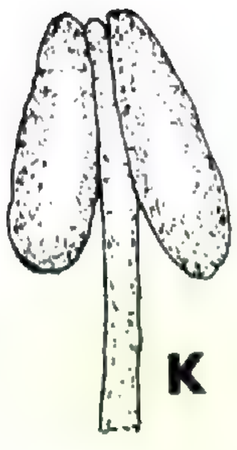
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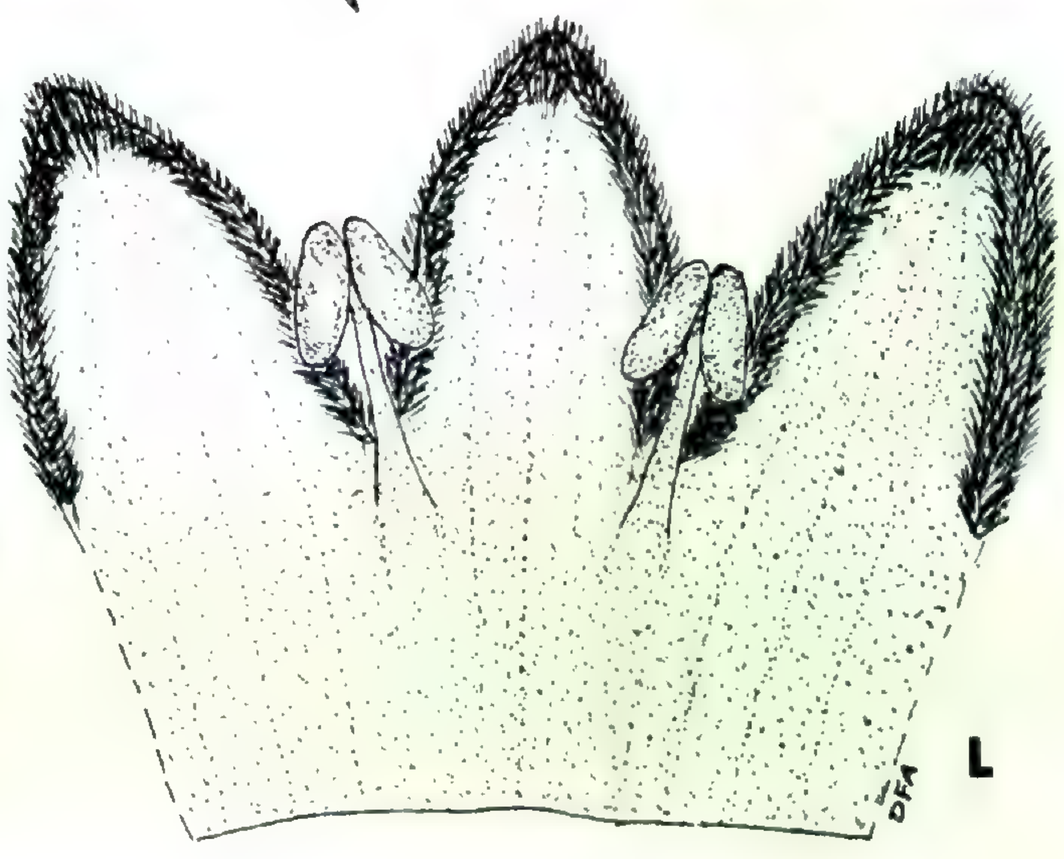
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the lobes reflexed at anthesis, tube and lobes densely pubescent outside; stamens excluded between corolla lobes, the filaments ca. 3 mm long, inserted at apex of corolla tube, glabrous, the anthers ca. 0.6 mm long, oblongoid; ovary ovoid, ca. 1.5 mm long, ca. 1.2 mm in diameter, villose, the style ca. 3 mm long, shortly lobed (almost imperceptibly) at apex, pubescent throughout, the stigmas 2, complanate and recurved to ± rounded. *Fruits* ellipsoid to elliptic-ovoid, 30–33 mm long, 17–18 mm in diameter, deeply rugose striate, light reddish-brown, the calyx reflexed at ca. 180°; seeds 1, ovoid, to 20 mm long, 13 mm in diameter.

Holotype: Brazil, Amazonas, prope Esperança ad ostium fluminis Javary, *Ducke RB 24413* RB; isotypes G, K, US.

Amazonas, Brazil; terra firme in high forest and capoeiras; flowering in April, and September to December; fruiting in October. Illustration: Fig. 38 A–D.

BRAZIL. AMAZONAS: Manaus, Estrada de Frances Novo, terreno firma, arenoso, capoeira fechada, alta, trepadeira volúvel, fr, 12.3.1956, *Dionizio & Chagas INPA 3592* (IAN). Esperança, ad ostium flum. Javary, silva non inundabili, fls albidis, 26.10.1942, *Ducke 1128* (IAN, MG, MO, NY, US). Cachoeira das Araras, Uaupes, cipó, estendendo-se para a margem do rio, 30.9.1945, *Froes 21305* (IAN, K). Uaupes, terra firme, high forest, light rosy fls, 15.4.1947, *Froes 22125* (IAN, U). Igarape Jandiatuba, fr, 12.1.1949, *Froes 23907* (IAN). Região do Rio Madeira, Rio Cunuma, Munic. Borba, mata virgem, terra firme alta, 11.11.1957, *Froes 33804* (IAN). Munic. São Paulo de Olivença, basin of cr Belém, terra firme, high forest, *Krukoff 8819* (BM, BR, G, MO, NY, U). Near Palmares, Munic. São Paulo de Olivença, *Krukoff 8557* (A, BR, G, MO, NY, U, US). Munic. São Paulo de Olivença, basin cr Belém, vine, terra firme, high forest, atypical, 26.10–11.12.1936, *Krukoff 9044* (A, BM, MO, NY). Rio Negro, Japatí, capoeira, cipó trepando em arvores grandes, 17.4.1947, *Pires 339* (IAN, NY).

VENEZUELA. BOLIVAR: Wooded slopes of Quebrada Oparumá, between Santa Teresita de Kavanayen & Río Picairao (tributary of Río Mouak), 1065–1220 m, 20–21.11.1944, *Steyermark 60396* (VEN).

Most specimens of this species exhibit the characteristic lanceolate-oblong leaves with acuminate to long acuminate apices and densely appressed reddish-brown indument below. *Dicranostyles sericea* and *D. guianensis* are the only other species with the indument of the lower leaf surface similar to *D. longifolia*. The leaf shape is usually distinctly different and provides a good criterion for their recognition; the length/width ratio of *D. longifolia* is usually all that is needed to separate them.

Dicranostyles longifolia, *D. guianensis*, and *D. villosus* all have very short stylar branches and stigmas which differ in some respects from the other members of the subgenus. The stigmas of these three species are commonly more flattened at the apex, and more obviously recurved and sheathing around the style than the other species. There are, however, some flowers of both *D. densa* and *D. costanensis* which exhibit this condition.

9. **Dicranostyles villosus** Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 250. 1922.

D. villosa Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 169. 1925, *sphalma*.

Lianas; stems grayish-brown, glabrous. *Leaves* with petioles 5–9 mm long, appressed pubescent; blades oblong to elliptic-oblong, 4–10 cm long and 2–4 cm wide, the base attenuate to rotund, the apex obtuse, shortly acuminate, chartaceous, the secondaries in 6–9 pairs; glabrescent. *Inflorescences* axillary,

racemose or cylindric-thyrsiform, villose; bracts ovate, ca. 0.5 mm long, membranaceous, persistent, glabrous or villose. *Flowers* with pedicels 1–2.5 mm long; sepals ovate, the outer lobes often acute, the inner lobes broadly ovate, the apex rounded to retuse, 1.5–2 mm long and 1.5–3 mm wide, the outside glabrous or densely pubescent; corolla white, subrotate but with a tube ca. 2 mm long, lobes 3–4 mm long, the lobes pubescent along outside margins, the apex villose without and within; stamens introrsely curved and included at corolla tube apex, the filaments 0.2–0.5 mm long, tapering from a glabrous base, inserted ca. 2 mm above corolla base at tube apex, the anthers ca. 0.3 mm long, subrotund to oblongoid; ovary obovoid, ca. 1 mm long, ca. 1.2 mm in diameter, glabrous, the style 1.2–2 mm long, with two short branches at the apex, the stigmas complanate or occasionally ± rounded. *Fruits* ovoid, 21–25 mm long, 10–14 mm in diameter, pericarp leathery to woody, wrinkled or smooth, becoming black, the calyx reflexed to ca. 180°; seeds 1, ovoid, 12–15 mm long, to 10 mm in diameter.

This species apparently has a disjunct distribution: the tautonymic variety is known only from Óbidos in western Pará, the var. *lasiocalyx* from the Surinam-French Guiana frontier. The varieties may be separated as follows:

a. Calyx and pedicels glabrous ..... 9a. *D. villosus* var. *villosus*
aa. Calyx and pedicels villose ..... 9b. *D. villosus* var. *lasiocalyx*

9a. **Dicranostyles villosus** var. **villosus**

Holotype: Brazil, Pará, Óbidos, flum. Rio Branco, ad locum Castanhal Grande, *Ducke MG 17116* RB; isotypes F, G, U, US.

Known only from the type collection in western Pará; in clay soil along the margin of the Rio Branco; flowering July.

9b. **Dicranostyles villosus** var. **lasiocalyx** A. Mennega, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 71: 551–554, *pl. I, fig. 1*; *pl. II.* 1968.

Holotype: French Guiana, Maroni River, anno 1864, *Melinon 114* P.

Nassau Mountains, Oelemari River, and Maroni River; in a xeromorphic forest with abundant lianas and epiphytes, and along the bank of the river; ca. 550 m; fruiting in March, with fruits probably maturing in April or May. Illustration: Proc. Kon. Ned. Akad. Wetensch., Ser. C. 71: 553, *pl. I, fig. 1*; *pl. II.* 1968; although the anthers appear to be basifixed in this illustration they are indeed versatile and introrsely bent.

SURINAM: In montibus qui dicuntur Nassau, plateau A, near km 8.2, berries dark green, 12.3.1949, *Lanjouw & Lindeman 2667* (U). Ca. portum aeronaut. ad flum. Oelemari, shrub 5 m tall, fr green, 19.3.1963, *Wessels Boer 999* (U).

Although known from two disjunct locations, the two varieties of this species show remarkable similarity. The plants from the Guianas are somewhat smaller than the Brazilian plant, and the pedicels of the Guianan plants are pubescent. Until more collections of this species are made it seems best to maintain the two recognized varieties.

This species is unique in the genus for its characteristically flattened stigmas which are flattened, apparently held at about 180°, and irregularly lobed around the margins. As in *Dicranostyles densa*, the anthers are introrsely bent. This condition is apparently rare in the family, being described only in the related genus *Humbertia* from Madagascar (Pinchon, 1945). *Humbertia* differs slightly in this condition, however, in having the anthers introrsely bent only while in bud.

Subgenus 2. **Kuhlmanniella** (Barroso) D. Austin, stat. et comb. nov.

Kuhlmanniella Barroso, Rodriguesia 9: 36. 1945, as genus. (Type: *D. falconiana* (Barroso) Ducke.)

10. **Dicranostyles falconiana** (Barroso) Ducke, Trop. Woods 90: 28. 1947.

Kuhlmanniella falconiana Barroso, Rodriguesia 9: 36. 1945.

Lianas; stems grayish-brown, smooth to slightly angled, glabrescent. *Leaves* with petioles 4–20 mm long; blades elliptic to oblong, 8–30 cm long and 6–18 cm wide, the base obtuse to ± truncate or cordate, occasionally unequal, the apex obtuse, acuminate, subcoriaceous, the secondaries in 6–12 pairs; glabrescent. *Inflorescences* axillary, paniculate-thyrsiform, occasionally with small leaves among cymes, glabrescent, drying black; bracts ovate, to ca. 1 mm long, glabrous. *Flowers* with pedicels 5–10 mm long; sepals ovate, ca. 1.8 mm long and ca. 1.5 mm wide, glabrous, drying black; corolla funnelform, white, 4–5 mm long, the lobes inflexed to erect at anthesis, the outside densely pubescent, the tube glabrous inside; stamens excluded between lobes, the filaments ca. 2 mm long, inserted at the apex of corolla tube, the tube glabrous inside, the anthers ca. 0.75 mm long, ± trianguloid; ovary ovoid, ca. 1.2 mm long, ca. 1 mm in diameter, densely villose, the style ca. 1 mm long, entire, the stigma cylindric-oblong, imperceptibly two-lobed. *Fruits* unknown.

Holotype: Brazil, Amazonas, Manaus, Estrada do Alexio, *Ducke RB 35591* RB.

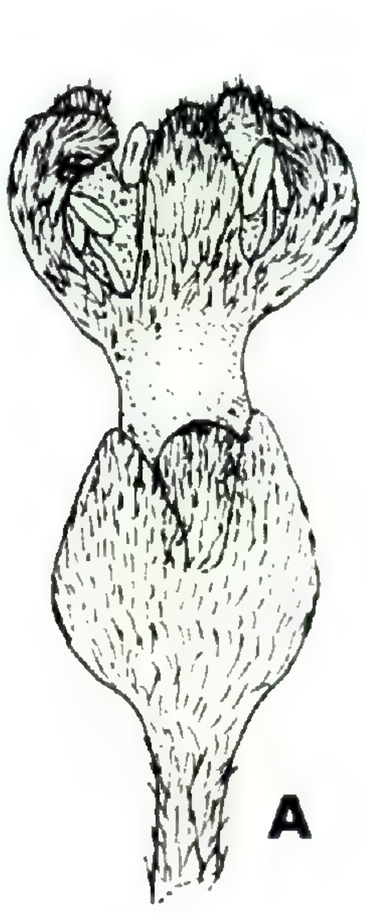
Known only from eastern Amazonas, Brazil; found on terra firme; flowering in September and October. Illustration: Rodriguesia 9, *fig. 1*.

BRAZIL. AMAZONAS: Munic. Borba, near Bella Vista, basin Rio Madeira, terra firme, 4–6.9.1934, *Krukoff 5970* (A, F, G, MO, NY, U).

Dicranostyles falconiana and *D. holostyla* are the only species in the genus with almost glabrous to glabrous leaves and inflorescences drying black. These two species can normally be separated by leaf size, for *D. falconiana* normally has quite large leaves. If they cannot be separated by this character, they may be recognized by flower dissections: *D. falconiana* has a cylindric stigma, completely pubescent ovary, and glabrous corolla tube, *D. holostyla* has an obpyriform stigma, only the upper part of the ovary pubescent, and a ring of glandular trichomes around the upper part of the corolla tube.

→

FIGURE 39. Flower structure of *Dicranostyles*.—A–D. *D. mildbraediana*.—A. Flower.—B. Dissected corolla.—C. Stigma-style-ovary length relations.—D. Gynoecium detail.—E–H. *D. holostyla*.—E. Flower.—F. Dissected corolla.—G. Gynoecium with sepals attached.—H. Gynoecium with sepals removed.—I–L. *D. integra*.—I. Flower.—J. Flower.—K. Dissected corolla.—L. Gynoecium detail.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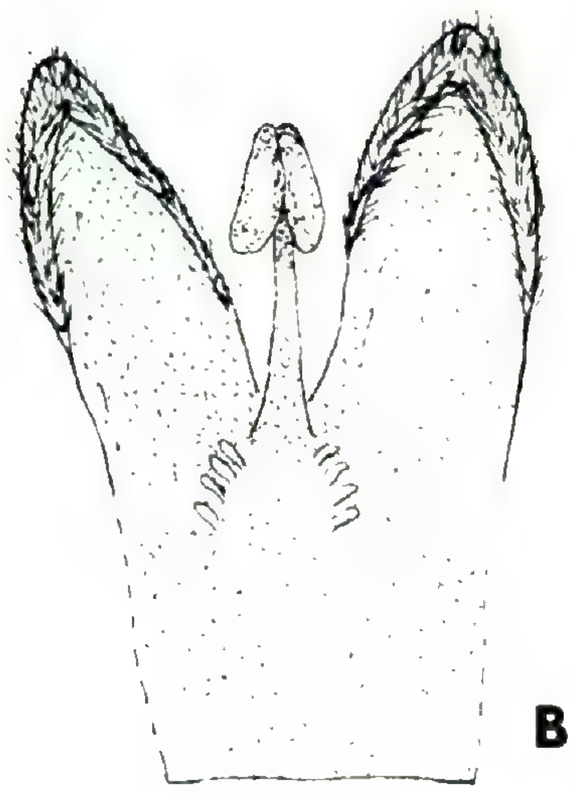
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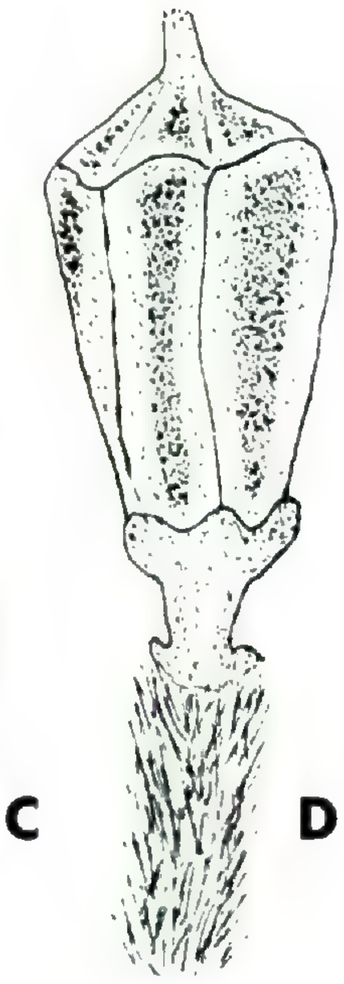
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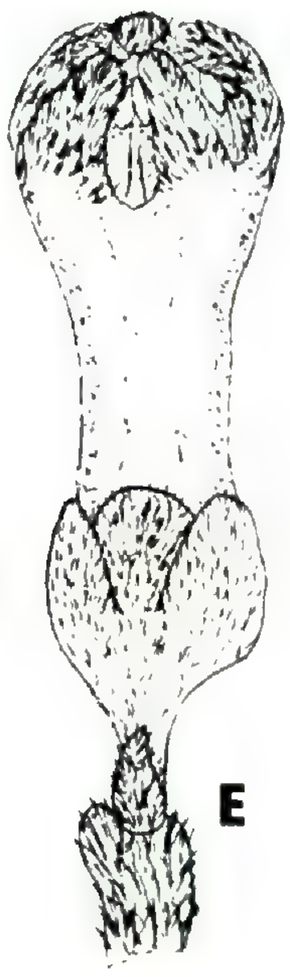
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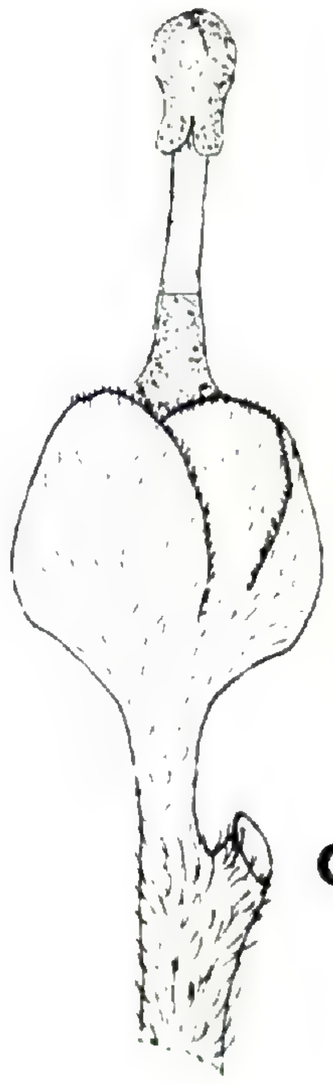
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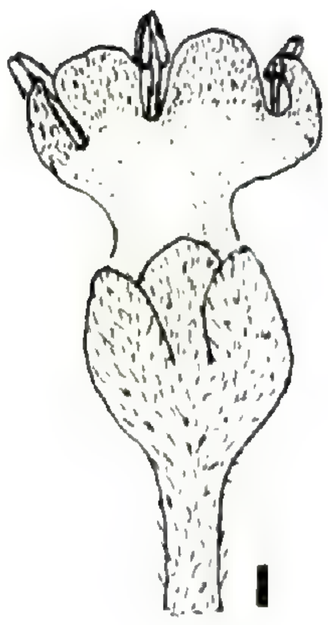
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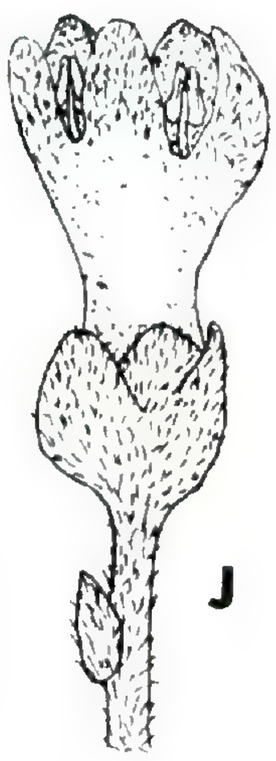
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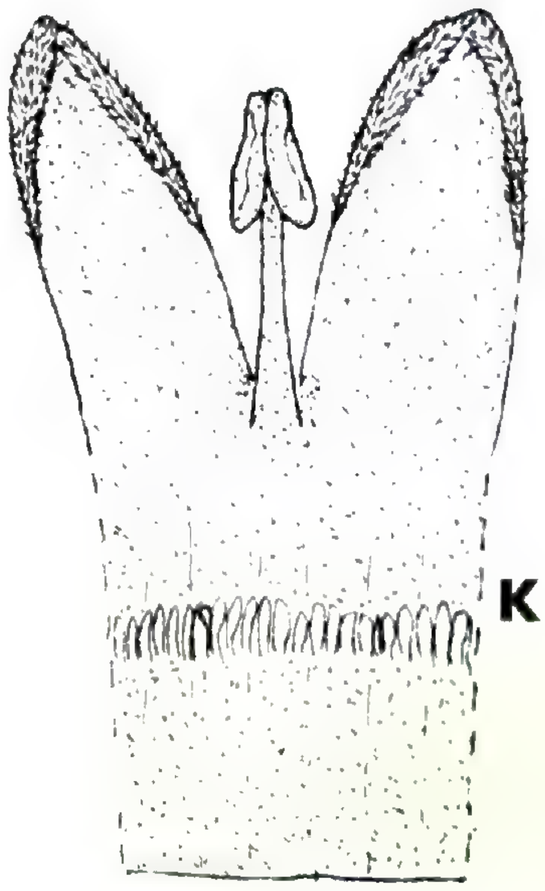
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11. **Dicranostyles holostyla** Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 69. 1925.

Kuhlmanniella holostyla (Ducke) Barroso, Rodriguesia 10: 21–24. 1948.

Lianas; stems grayish-brown. *Leaves* with petioles 10–15 mm long, appressed puberulous; blades lanceolate, occasionally elliptic, 7–15 cm long and 1.5–5.5 cm wide, the base obtuse, the apex acuminate, chartaceous, the secondaries in 15–20 pairs; glabrescent. *Inflorescences* axillary, cylindric-thyrsiform, solitary to fasciculate, appressed pubescent with whitish indument; bracts ovate, ca. 0.5 mm long, appressed white pubescent. *Flowers* with pedicels ca. 2 mm long; sepals broadly ovate, the outer lobes acute, the inner lobes rounded, 1–1.1 mm long and ca. 1.2 mm wide, scattered white pubescence outside, tips of outer sepals villose at tip, inner sepals pubescent only on exposed surfaces; corolla funnelform, white, 4–5 mm long, the lobes densely pubescent on upper half with scattered indument on lower half, the lobes inflexed at anthesis, the tube with shaggy glandular hairs ca. 2 mm from inside base; stamens excluded between corolla lobes, the filaments ca. 2 mm long, inserted at corolla tube apex, the anthers ca. 0.75 mm long, ± trianguloid; ovary ovoid, ca. 1.2 mm long, ca. 1 mm in diameter, the apex villose, the style ca. 1.2 mm long, entire, the stigma obpyriform, ca. 0.5 mm long, imperceptibly 2-lobed. *Fruits* long ellipsoid, 25–42 mm long, 14–15 mm in diameter, the pericarp leathery to woody, somewhat wrinkled, black.

Holotype: Brazil, Pará, prope Breves, *Ducke RB 18003* RB; isotypes K, US, IAN.

Common name: "Cipó abiú" (São Gabriel, Brazil—*Froes*), apparently alluding to the similarity between the leaves of the "Abiú" (*Pouteria caimito* (Ruiz & Pavon) Radlk.) and the vine. Illustration: Fig. 39E–H.

BRAZIL. ACRE: Near mouth Rio Macauhan, tributary of Rio Yaco, terra firme, buds, 5.9.1933, *Krukoff 5796* (BM, F, G, IAN, MO, NY, RB, U). AMAZONAS: Maues, mata da terra firme, argilosa, 7.10.1929, *Ducke RB 22574* (IAN, RB). Rio Negro, Curucuhy, high land, high forest, sand soil, fls green white, frts, 15.4.1947, *Froes 22154* (IAN). São Gabriel, Rio Negro, terreno silicoso, beira do rio, fls ferruginea branca, "cipó abiú," 9.10.1945, *Froes 21132* (F, IAN, K, NY, U). Rio Negro, Padauiry, Castanha, terra firme, high forest, low land, frts, 7.10.1947, *Froes 22536* (IAN). Munic. Borba, near Bella Vista, basin Rio Madeira, terra firme, 4–6.9.1934, *Krukoff 5975* (A, BR, F, G, MO, NY, U, US). Munic. Humayata, near Livramento on Rio Livramento, basin Rio Madeira, *Krukoff 6755* (A, BM, BR, G, MO, NY, U, US). Munic. São Paulo de Olivença, near Palmares, high land, 11.9–26.10.1936, *Krukoff 8559* (A, BM, BR, G, MO, NY, U, US). Rio Preto, solo argiloso, frts verdes, *Rodrigues & Lima 4162* (INPA, RB).

PERU. LORETO: Iquitos, silva, fls esverdeadas, 26.2.1924, *Kuhlmann 1504, RB 22497* (G, IAN, RB, US).

For similar species, see *Dicranostyles falconiana.*

12. **Dicranostyles integra** Ducke, Arq. Inst. Biol. Veg. 2: 68. 1935.

Lianas; stems grayish-brown to brown. *Leaves* with petioles 10–20 mm long; blades oblong, elliptic to ovate, rarely obovate, 9–16 cm long and 3–6 cm wide, the base obtuse, the apex acuminate, chartaceous, the secondaries in 12–19 pairs; glabrescent above, densely white pubescent below. *Inflorescences* axillary, cylindric-thyrsiform, 3–8 cm long, solitary or fasciculate, appressed white pubescent; bracts ovate, ca. 0.5 mm long, white pubescent. *Flowers* with pedicels

2–3(–5, *fide* Ducke) mm long; sepals broadly ovate to rotund, acute, 1.8–2.5 mm long and 2.2–2.5 mm wide, the outer lobes villose at apex, the inner lobes with villose mucrone, and membranaceous, margins glabrous but ciliate; corolla funnelform, white 4–5 mm long, the lobes inflexed at anthesis, the outside densely pubescent, a ring of shaggy glandular hairs in tube ca. 2 mm from corolla base; stamens excluded between corolla lobes, the filaments ca. 1–1.5 mm long, inserted at apex of corolla tube, the anthers ca. 0.5 mm long, ± trianguloid; ovary ovoid, ca. 2 mm long, ca. 1.5 mm in diameter, the apex villose, the style ca. 1.5 mm long, entire, pubescent on the lower half, the stigma obpyriform, ca. 0.5 mm long, imperceptibly two-lobed. *Fruits* unknown.

Holotype: Brazil, Amazonas, Estrada do Aleixo, Manaus, *Ducke RB 24410* RB; istotypes G, K, US.

Known only from Amazonas, Brazil; forest on terra firme; flowering August to December; fruiting period unknown but probably January to July. Illustration: Fig. 39, I–L.

Brazil. amazonas: Borba, mata da terra firme, fls brancas, 26.8.1942, *Ducke 1002* (GH, IAN, MG, MO, NY, US). Manaus, NE de Flores, corola brancacenta, 14.9.1945, *Ducke 1757* (A, F, IAN, K, MG, NY, US).

Colombia. amazonas: Vaupes, Río Apaporis, Jingojé, 13.6.1952, *Schultes & Cabrera 15479* (C).

This is the only species with densely appressed white indument on the lower leaf surface and the inflorescence in addition to an obpyriform stigma and a funnelform corolla.

13. **Dicranostyles mildbraediana** Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 11: 1150. 1927.

Kuhlmanniella mildbraediana (Pilger) Barroso, Rodriguesia 9: 36. 1948.

Lianas; stems grayish to grayish-brown. *Leaves* with petioles to 20 mm long; blades ovate, obovate, elliptic or lanceolate, 10–13 cm long and 3–4 cm wide, the bases mostly acute, rarely rounded to truncate, the apex acuminate, chartaceous, the secondaries 10–14 pairs; glabrescent above and below. *Inflorescences* axillary, cylindric-thyrsiform, solitary to fasciculate, white pubescent; bracts ovate, ca. 1 mm long, white pubescent. *Flowers* with pedicels 1–1.5 mm long; sepals ovate to broadly ovate, the apex acute, rounded or truncate, ca. 1 mm long and 1–2 mm wide, the outer lobes pubescent outside but with glabrous margins, the inner lobes appressed pubescent on exposed surfaces, glabrous on unexposed surfaces; corolla funnelform, 3–4.5 mm long, the lobes inflexed at anthesis, a ring of shaggy glandular trichomes near tube apex, the outside pubescent; stamens excluded between corolla lobes, the filaments ca. 1.5 mm long, inserted at apex of corolla tube, the anthers ca. 0.6 mm long, trianguloid; ovary obovoid, ca. 1.3 mm long, ca. 1 mm in diameter, glabrous, the style ca. 0.5 mm long, entire, glabrous, the stigmas obpyriform, imperceptibly two-lobed. *Fruits* unknown.

Holotype: Peru, Loreto, oberer Marañon, *Tessmann 4069* B†.

Lectotype: photo of *Tessmann 4069* MO.

Loreto, Peru; forest, terra firme, high forest; 160–220 m; flowering in March and September. Illustration: Fig. 39A–D.

PERU. LORETO: Balsapuerto, ca. 220 m, forest, 3.1933, *Klug 2947* (BM, F, G, GH, MO, NY, US).

While very similar to *Dicranostyles integra*, *D. mildbraediana* has leaves which are glabrescent on the lower surface. The most characteristic features of *D. mildbraediana* are the obpyriform stigma, short style, and obovoid ovary.

According to Mennega (1968; personal communication, 1968) there is a wood sample of the type collection in Reinbek, Germany (BFA 2744). The holotype was destroyed during the war, and no duplicates have been located. However, there is a photograph of the Berlin specimen at MO. The photograph permits a ready identification and, since a wood sample seems insufficient for designation as lectotype, is chosen as the lectotype.

14. **Dicranostyles laxa** Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 590. 1932.

Kuhlmanniella laxa (Ducke) Barroso, Rodriguesia 10: 21–24. 1945.

Lianas; smaller stems with persistent harsh indument. *Leaves* with petioles to 10 mm long; blades oblong to obovate-oblong, 6–11 cm long and 2–4 cm wide, the base acute to rounded, the apex obtuse, shortly acuminate, chartaceous, the secondaries in 8–10 pairs; with stiff, erect, unicellular indument on petioles, costa, laterals and scattered on blades. *Inflorescences* axillary, racemose to narrowly cylindric-thyrsiform with only the lower branches cymose, to 6 cm long, pubescent; bracts ovate, ca. 1.5 mm long, densely pubescent. Mature *flowers* not examined; pedicels to 3 mm long; sepals ovate, the apex rounded, 2 mm long, white- to yellow-pubescent; corolla campanulate-funnelform, white, ca. 3.5 mm long, the lobes triangular, the style entire, the stigma two-lobed. *Fruits* obovate to cylindric, 20–30 mm long, to 15 mm in diameter, pericarp thin, woody, striate, gray mottled to black, the calyx reflexed to ca. 180°; seeds 1–4, ovoid to trigonous, to ca. 15 mm long, to ca. 8 mm in diameter.

Lectotype: Brazil, Amazonas, loco Varadouro do Morcêgo prope fluvium Madeira inferiorem, *Kuhlmann 311*, *RB 22493* RB; isolectotypes B†, US.

Known only from the Uaupes—Rio Negro area in Amazonas, Brazil; in sandy margins (várzea) of rivers; flowering in October and November; fruiting March.

BRAZIL. AMAZONAS: Rio Negro super. ad ostium flum. Uaupes, margem arenoso, 1.11.1932, *Ducke RB 24408* (G, RB). Santo Antonio do Içа, São Paulo de Olivença, Igarape de Belém, sterile, *Froes 20747* (RB); Manaus-Itacoatiara, km 170, picada XXII, a 380 m da estrada, fls cremes, *Rodrigues 7265* (INPA, RB). Manaus, Igarape de Belém, habitat argiloso, frs verdes, *Pessoal do C.P.F. INPA 6144* (INPA, MG).

Dicranostyles laxa and *D. globostigma* are the only species in the genus with erect trichomes on the lower leaf surface. The pubescent younger stems and petioles immediately distinguish *D. laxa* from *D. globostigma*. This pubescence often persists in fruiting plants and is distinctive of the species.

Although I examined the holotype deposited at Rio de Janeiro (RB), time did not permit an examination of a dissected flower. Therefore, the data provided on flower structure is little more than that published by Ducke.

15. **Dicranostyles globostigma** D. Austin, sp. nov.

A *D. laxis* similis sed foliis maioribus, trichomatibus minoribus et minus rigidis, ea inflorescentiarum adpressis distincta est. A speciebus aliis in subg. *Kuhlmanniella* stigmatibus globosis distinguenda; a *D. sericea* in subg. *Dicranostyles* stigmatis plus minusve globosis similis sed tubis lobis corollarum aequalis et filamentis basis trichomatibus glandiferis differunt.

Lianas; stems brownish-black, angular, the bark somewhat scaly. *Leaves* with petioles 25–35 mm long, rugulate, glabrescent; blades elliptic, 16–19 cm long and 7–10 cm wide, the base broadly obtuse, the apex obtuse, acuminate, coriaceous, the veins deeply sunken above and very prominent below, the secondaries in 9–10 pairs; glabrous above, the veins and surface covered with erect, spaced rusty indumentum. *Inflorescences* axilliary, subracemose-thyrsiform, ca. 4 cm long, pubescent with a rusty indument. *Flowers* with pedicels ca. 2 mm long; sepals deltoid-ovate to suborbicular, the outer lobes acute, the inner rounded, ca. 2 mm long, 1.5–2 mm wide, appressed ferrugineous puberulent; corolla subfunnelform, reddish (probably due to indument), ca. 4 mm long, glabrous inside, the lobes pubescent outside, the tube glabrous; stamens excluded between corolla lobes, the filaments ca. 1 mm long, inserted ca. 2 mm above corolla base at tube apex, glabrous, the anthers ca. 0.75 mm long, trianguloid; ovary conic-ovoid, ca. 1 mm long, ca. 0.75 mm in diameter, densely pubescent with erect trichomes ca. 0.33 mm long, the style entire, ca. 0.75 mm long, the stigma globose and capitate, imperceptibly two-lobed. *Fruits* unknown.

Holotype: Brazil, Amazonas, Tapurucoara, Rio Negro, cipó altão, fl ferrugineas, 8.4.1947, *Pires 249* (NY, IAN?).

Known only from type collection (Fig. 38E–L, 44).

This species and *Dicranostyles laxa* are very closely related and show many characteristics which are considerably more advanced than the other species of the subgenus. The large coriaceous leaves and glabrous stems distinguish the species from *D. laxa*.

3. **Lysiostyles**

Lysiostyles Benth., London Jour. Bot. 5: 356. 1846.

Monotypic.

Lysiostyles scandens Benth., London Jour. Bot. 5: 356. 1846.

L. pubescens Gleason, Bull. Torrey Bot. Club 54: 616. 1929. (Holotype: Guyana, *Persaud 67* NY; isotype K).
L. scandens var. *latifolia* Benth., London Jour. Bot. 5: 356. 1846. (Holotype: *Schomburgk 763(1532)* K; isotypes F, W, P, not seen).

Lianas reaching 30 m; stems 3.8 cm in diameter or larger; young branches red pubescent, the older branches grayish to brownish, irregularly angled, glabrous, the bark somewhat scaly, the pith ± round in cross-section, light brown. Leaves alternate, simple; petioles canaliculate; blades oblong to elliptic or obovate, 7.5–14 cm long and 5–10 cm wide, the base obtuse, the margins entire, the apex shortly acuminate, coriaceous; venation brochidodromus; glabrescent above, densely reddish pubescent below. *Inflorescences* axillary, slender cylindric-

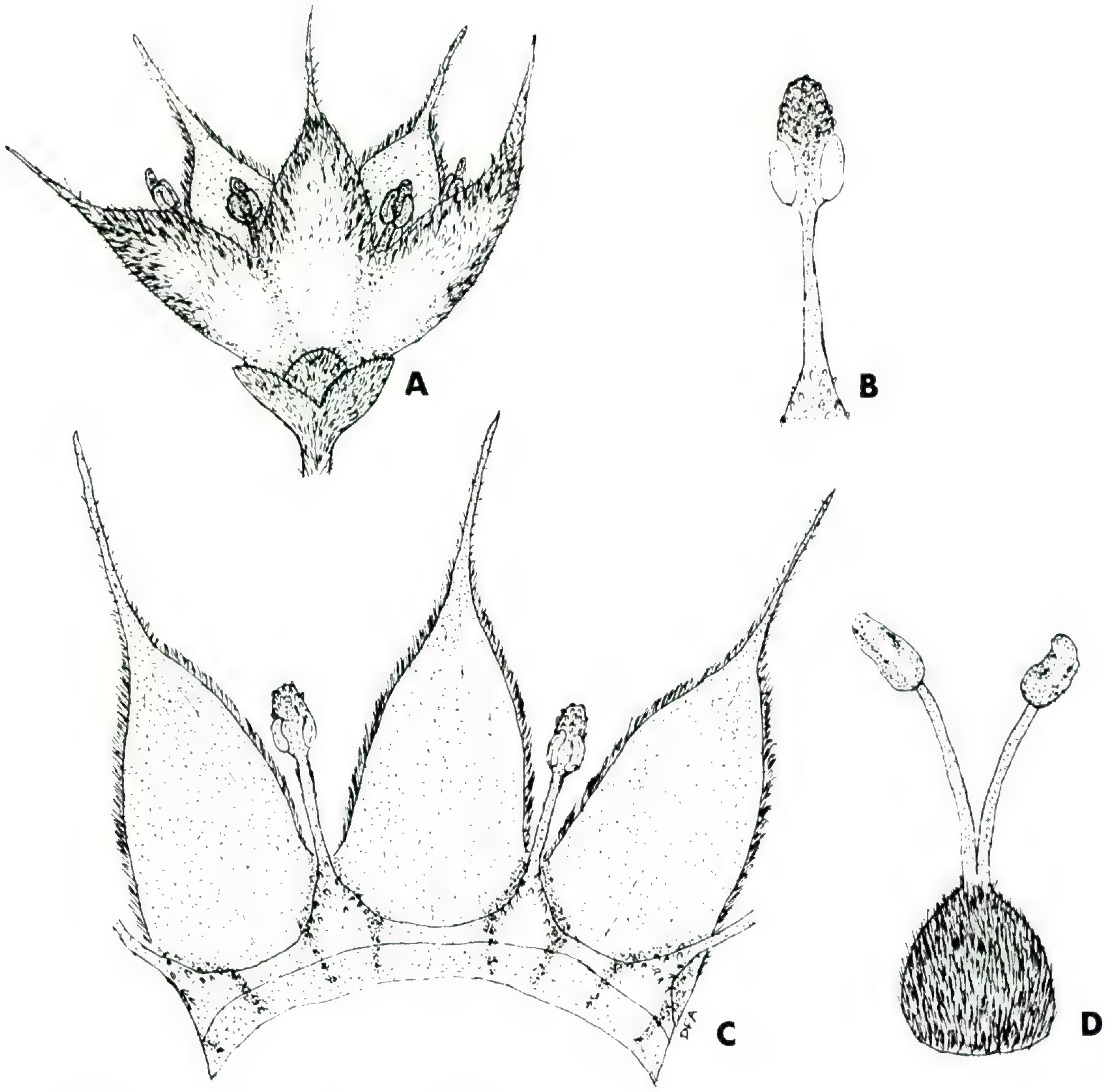


FIGURE 40. Flower detail of *Lysiostyles scandens*.—A. Flower at anthesis.—B. Stamen with broad glandular connective and dilate-triangular filament base.—C. Corolla dissection.—D. Gynoecium detail.

thyrsiform, 2.5–8 cm long, often racemose below and cymose above, dichasia 2–5-flowered, the rachis and branches densely red pubescent; bracts triangular, densely red pubescent. *Flowers* actinomorphic, pentamerous, sweet-scented; sepals broadly ovate to orbicular, the outer lobes acute, the inner lobes obtuse, about equal in length, red pubescent; corolla subrotate, white, the tube ca. 2 mm long, glabrous, the lobes 4–6 mm long, triangular, acute, terminating in a long acuminate, almost filiform apex, the outside villose, the inside glabrous; stamens shortly excerted between corolla lobes, epipetalous, shorter than lobes of corolla, glabrous, filament ca. 1 mm long, the bases triangular, connected into a ring, the anthers with oblong, obtuse flattened connective 1–1.5 mm long, the thecae on basal lobes of connective, ca. ½ as long as connective, functionally extrorsely dehiscent; ovary depressed-globose, ca. 1 mm long, ca. 1 mm in diameter, in-

FIGURES 41–42. Types of *Maripa*.—41. Holotype of *M. janusiana* (*Klug 809*, US).—42. Holotype of *M. pauciflora* (*Sprague 142*, K).

completely bilocular with a partial septum in lower portion, villose, the ovules 4, the styles fused to completely free, ca. 1 mm long, glabrous, the stigmas 2, capitate, spherical to short-cylindrical, white when living. *Fruits* nut-like, woody, indehiscent, one-locular, globose to oblong-globose, 2.5 cm long, 2.3 cm in diameter, the pericarp hard, the surface ruminate, buff-gray; seeds 1 through abortion, ellipsoid to oblong-ellipsoid, 16–18 mm long, 14–15 mm in diameter, glabrous, surrounded by dark perisperm, the seed coat coriaceous, the albumen absent or very scanty, the embryo with the radicle folded against the lower part of the latiplicate incumbent cotyledons, ca. 15 mm long.

Holotype: Guyana, Maboodahu, *Schomburgk 491* (*1st coll.*) K. isotypes G, W, photo MO.

Pollen 3-colpate, prolate; chromosomes unknown; flowering peak in June and July but flowering through December; seeds possibly used as in *Maripa*.

Common name: "Melocotón" (Delta Amacuro, Venezuela—*Blanco*).

Eastern Estado Bolívar and Territory Delta Amacuro, Venezuela, Guyana and Surinam; summit of cerro La Paloma, rainforest, Mora forest, clump-Wallaba forest, mixed forest; sea level to 200 m; flowering June to December; fruiting October and November. Illustration: Fig. 40.

GUYANA. Bootooba, *Persaud 200* (F). Essequibo River, Moraballi Creek, near Bartica, *Sandwith 297* (G, K, NY, US, U), *601* (K, NY, US, U). Guyane Anglaise, *Schomburgk 831(763)* (BM, G). Cuyuni River, Oko Creek. *Tutin 319* (BM, K, US, U). Cuyuni River, Arawak Matope, *Tutin 415* (US, U). Bartica-Potaro Road, ca. 83 miles, *Tutin 207* (BM, K, US, U). Winiperu Creek, Essequibo River, *For. Dept. Br. Gui. 3026* (F, K, NY).

SURINAM. Brokopondo District, 10 km NW of village Brokopondo, *v. Donselaar 3484* (U).

VENEZUELA. BOLIVAR: Río Toro (Río Grande), between Río La Reforma & Puerto Rico, N of El Palmar, between junction with Río Reforma & 1 km below junction, *Steyermark 88128* (NY, U, VEN). DELTA AMACURO: Río Cuyubini, Cerro La Paloma, Sierra Imataca, *Steyermark 87602* (NY, US, U, VEN). E of Río Grande, E-NE of El Palmar, ca. de los limites del Estado Bolívar, *Blanco 150* (VEN).

E. EXCLUDED AND DOUBTFUL SPECIES

1. *Maripa acuminata* Rusby, Descr. South Amer. Pl. 102. 1920. (Holotype *H. H. Smith 877* NY: isotype US).

= *Bonamia trichantha* Hall. f., Bot. Jahrb. Syst. 16: 528. 1893. (Type *Triana 2146* G, not seen). See Austin (1970).

2. *Maripa spectabilis* Choisy *in* DC., Prodr. 9: 327. 1845. (Lectotype *Martius s.n.* M).

Correct name: *Bonamia maripoides* Hall. f., Bot. Jahrb. Syst. 16: 529. 1893; additional synonyms = *Prevostea spectabilis* (Choisy) Meisn *in* Mart., Fl. Bras. 7: 325. 1869; = *Calycobolus spectabilis* (Choisy) House, Bull. Torrey Bot. Club 34: 146. 1907. See Austin (1970).

3. *Maripa villosa* Sprengel *in* L., Syst. Veg. 1: 643. 1825. (Type: Brazil, *Sello s.n.* B).

Apparently only two authors since Sprengel have seen the collection on which this species was based, namely G. Don and H. Hallier. Don (1838) listed the species and stated that it was growing in the greenhouse where he saw it. His description is insufficient for a positive determination as was Sprengel's. Hallier (1893) also listed the species and commented that it must be excluded from the family because, "it has typically opposite leaves and habitually no similarity at all with any Convolvulaceae, least of all with *Maripa*." (Hallier, 1893: 526, translation by Mrs. Carla Lange).

Because of Hallier's comments the species is excluded from *Maripa* as was previously done by Gleason (1929) and Falcão (1945). Unfortunately there are insufficient data available to suggest the correct relations.

4. *Maripa volubilis* Pittier, Bol. Soc. Venez. Ci. Nat. 6: 199. 1940. (Lectotype here designated: *Pittier 14381* US).

Synonyms include *Jacquemontia hirtiflora* (Martens & Galeotti) O'Donell, Anales Inst. Biol. Univ. Nac. México 12: 82–83. 1941; *Ipomoea hirtiflora* Martens & Galeotti, Bull. Acad. Roy. Brux. 13: 13. 1845; *Jacquemontia lactescens* Seemann, Bot. Voy. Herald 171–172. 1854; *J. pereyana* (Duchass & Walpers) Standley, Fl. Panama Canal Zone, Contr. U.S. Natl. Herb. 27: 313. 1928.

This species belongs to neither *Maripa* nor *Jacquemontia*. It has several characters in common with *Merremia* and *Hewittia*, but *Maripa volubilis* does not seem to fit either of these genera either. Robertson (personal communication, 1970) thinks that a new genus may have to be described for the species.

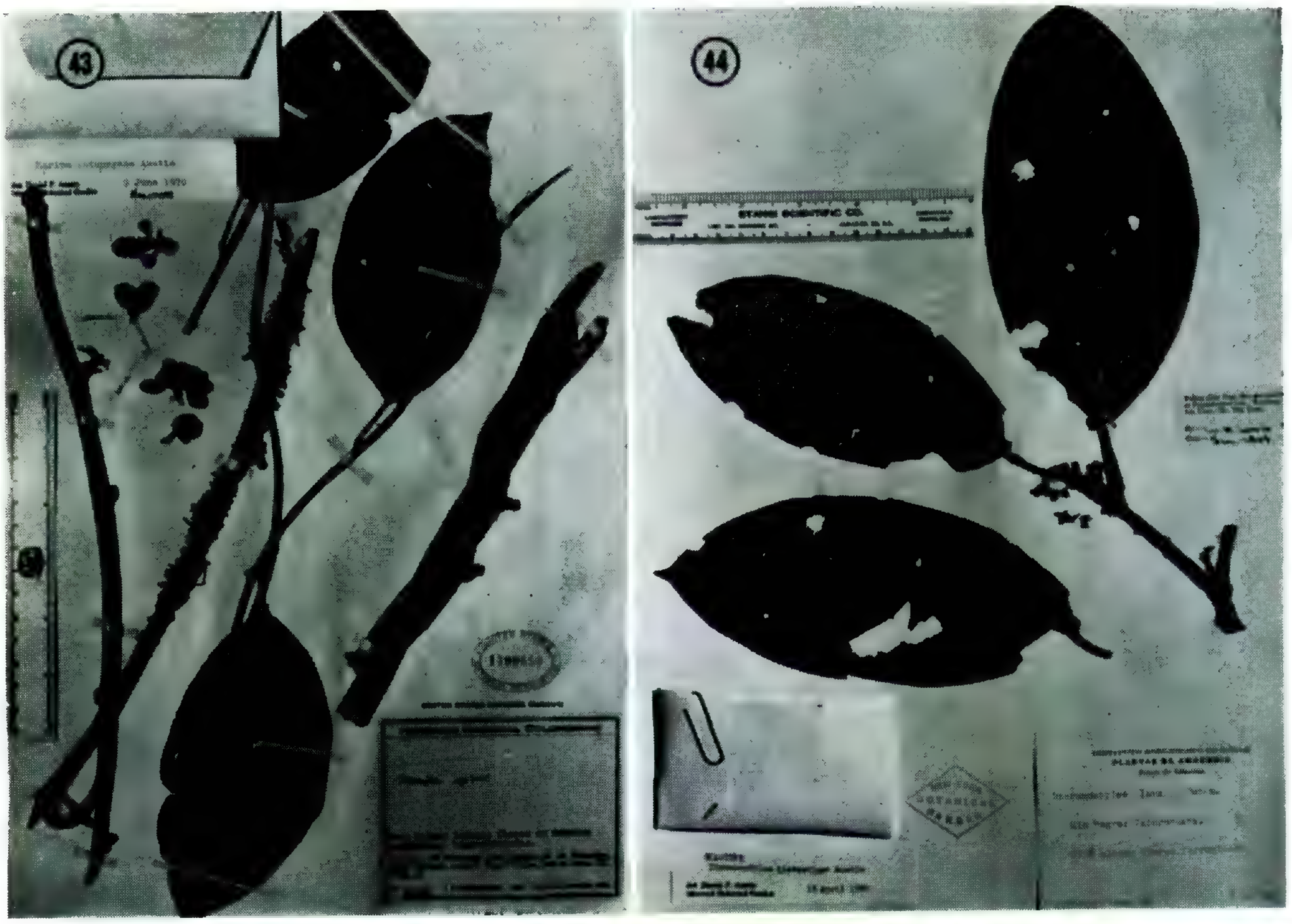
Curiously Pittier cited a type for every new species except this one. The specimen deposited at US and annotated by its collector is selected as lectotype.

5. *Maripa decemlobata* Stuck *ex* Seckt, Fl. Cordobensis 1929–30, *nom. illeg. pro syn.*

Synonyms include *Ipomoea megapotamica* Choisy *in* DC., Prodr. 9: 375. 1845. (Type: Uruguay, *Otto s.n.* G, not seen, IDC-micro fische seen); *Argyreia megapotamica* (Choisy) Grisebach, Abh. Königl. Ges. Wiss. Göttingen 24: 263. 1879; *Murucoa megapotamica* (Choisy) O. Kuntze, Rev. Gen. Pl. 3: 217. 1893. See O'Donell (1948).

6. *Murucoa hieronymi* O. Kuntze, Rev. Gen. Pl. 3: 217. 1893. (Type *Lorentz & Hieronymus 220*, photo seen).

Synonyms include *Ipomoea hieronymi* (Kuntze) O'Donell, Lilloa 14: 169–192. 1948; *Argyreia megapotamica* var. *puberula* Grisebach, Symb. 263. 1879; *A. hieronymi* (Kuntze) K. Schumann, Just's Bot. Jahresber. 1: 383. 1900. See O'Donell (1948).



FIGURES 43–44. Types of *Maripa* and *Dicranostyles*.—43. Holotype of *Maripa putumayana* (*Cuatrecasas 10736*, US).—44. Holotype of *Dicranostyles globostigma* (*Pires 249*, NY).

7. *Murucoa juramenti* O. Kuntze, Rev. Gen. Pl. 3: 217. 1893. Type *Lorentz & Hieronymus 285*, photo seen).

Synonyms include *Ipomoea juramenti* (Kuntze) O'Donell, Lilloa 14: 169–192. 1948; *Argyreia juramenti* (Kuntze) K. Schumann, Just's Bot. Jahresber. 1:383. 1900. See O'Donell (1948).

8. *Lysiostyles sericea* Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 322. 1931. (Holotype *Chickering 130* F; isotype G).

Correct name: *Itzaea sericea* (Standl.) Stanley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 83. 1944. Additional synonymy: *Bonamia brevipedicellata* Myint & Ward, Phytologia 17: 188–191. 1968. (Holotype *Schipp 1210* GH; isotype G).

Standley and Steyermark established this new genus with reservation, but they felt that this species was different from anything else known from the Convolvulaceae. Specimens without fruits are superficially little different from *Bonamia*, as witnessed by Myint and Ward. The fruits of this species are somewhat similar to those of *Bonamia maripoides*, and Myint and Ward felt that the flowering material was also similar to this species. Yet the unique endocarp structure of the fruits, the red seeds, and the arrangement of the petiole and laminar vasculature have led me to follow Standley & Steyermark. See Austin (1971*a*).

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NOTES ON CENTRAL AMERICAN MARANTACEAE I. NEW SPECIES AND RECORDS FROM PANAMÁ AND COSTA RICA[1]

HELEN KENNEDY[2]

ABSTRACT

Four new species of *Calathea* (Marantaceae) are described from Costa Rica and central Panamá. Synonymies and misidentifications are discussed. Data on pollination are given.

The large herbaceous monocots, especially the Scitamineae, are a conspicuous element of most lowland semi-deciduous to wet tropical forests. In spite of their showy nature they are poorly known. In Central America they flower primarily during the rainy season when many roads are impassable, thus discouraging many collectors. Since they are frequently bulky and awkward to press, they may be purposely overlooked by botanists. Their most important and distinctive features, the habit of growth, form of the inflorescence and flowers, are commonly obscured or lost in herbarium specimens, thus abetting misidentification and confusion and making field work essential for their understanding. While working on the pollination of the family Marantaceae, it became evident that a large part of the Costa Rican and Panamanian species were undescribed. There are 23 species recorded in the *Flora of Panama*; to date I have found 19 additional undescribed or unrecorded species of Marantaceae in Panamá. In *Calathea* alone, there are an additional 16 species, 11 of which are undescribed. Surprisingly, all but two are from central Panamá: Cerro Jefe and La Eneida, Cerro Campana, Santa Rita Ridge and Río Guanche, near Portobelo. On the lower Río Guanche alone, there are seven undescribed Marantaceae. To be sure, several of these and the species from Santa Rita are decidedly South American (Colombian and upper Amazonian) in affinity, and undescribed from there either. There are surely other new species yet to be found in the Atlantic coastal forests, the Osa Peninsula, Costa Rica, and the mountains of Darién, Panamá.

The Marantaceae may always be recognized vegetatively, from seedling stage onward, by the pulvinus (a region of specialized cells just below the leaf blade) and the major (longitudinal) veins which form a sigmoid curve with evenly spaced, parallel transverse veins between them and at right angles to them (these seen if the leaf is held up to the light) (Tomlinson, 1961: 62). Florally the family is characterized by the spring mechanism of the style and stigma. The showy portion of the flower usually consists of the sterilized, often petaloid, staminodes (see Fig. 1c): outer staminode, callose staminode, and the cucullate staminode which holds the style in place before pollination. While in bud the pollen is transferred from the anther to a depression (see Fig. 1c) in the style immediately

[1] I wish to thank Dr. Robert L. Dressler for showing me several new species localities, for reading the manuscript, and for assistance and guidance without which this study would not have been possible; Robin Foster for showing me the Rio Guanche site and for use of his vehicle for field work; Drs. R. L. Wilbur and G. L. Webster for reading parts of the manuscript; and Dr. Robin Andrews for help in typing the manuscript.

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ANN. MISSOURI BOT. GARD. 60: 413–426. 1973.

behind the cup-like terminal stigma. During pollination, the pollinator (bees of the genus *Calathea*) inserts the head and proboscis or proboscis (beak?) only into the flower displacing the cucullate appendage and thus releasing the style which is under tension. It snaps upward (and slightly sideways in *Maranta*, *Ctenanthe*, and *Thalia*) bringing the stigma into contact with the pollen previously deposited on the pollinator's body and simultaneously depositing its own pollen in the same place. The style then comes to rest against the callose staminode (see Fig. 1c). In the case of *Calathea* the pollen is deposited in the proboscidial fossa. The flowers normally open spontaneously (see Figs. 1c and 3c), but there is also a group in which the buds remain closed (see Fig. 4b) until forcibly opened by the bee. The latter situation prevails in one group of Calatheas corresponding to a portion of the series Scapifoliae of Schumann (1902). This very specialized condition is quite distinct from cleistogamy. There are a few which are truly cleistogamous, notably *Calathea panamensis* Rowlee *ex* Standl., but they are not closely related to the above mentioned group. In the great majority of Marantaceae species it is mechanically impossible to get pollen in the stigma of the same flower, however, certain species of *Maranta* appear to be exceptions to this rule.

Calathea dressleri H. Kennedy, sp. nov.—FIGURE 1.

Acaulis. Planta ad 45 cm alta. Folia ad 2 cm longa petiolata, petioli pars superior ad 1.5 cm longa complanata callosa supra puberula obovata vel late elliptica raro suborbiculata basi acuta vel obtusa supra glabra splendens prope medianum minutissime puberula obscure viridia et prope medianum pallidius maculata subtus pallide viridia vel atroviolacea; vagina subglabra ad 19 cm longa. Spica e rhizomate capitata subglobosa ad 5.5 cm longa et ad 5 cm diametro pedunculo 5–23.5 cm longo subglabro sustenta; bracteae 14–17 spiraliter dispositae ovatae vel late lanceolatae 2.45–3.5 cm longae et 1.5–2.7 cm latae herbacea intus albae vel pallidae violacea extus pallidae violacea obtusae apice recurvata, laxius imbricata; paria florium 3 bracteolis indurato-claviculatis exsertis et mesophyllis comitata; ovarium glabrum album 1.3–1.7 mm longum; sepala 19 mm longa et 2.5–3 mm lata, lineari-lanceolata glabra; corollae tubus 23 mm longus albus vel subviolaceus glabrus, lobi ovati vel lanceolate 9–13 mm longi et 4.5–5.3 mm; staminodium exterius album vel subviolaceum late ovatum vel orbicularum emarginatum 9 mm longum et 6 mm latum; callosum spatulatum 1 cm longum et 0.8 cm latum; cucullatum 7 mm longum. Capsula 9–10 mm longa calyce demum coronata; semina trigona dorso rotundata rugosa, arillo lamelloso albo.

Rosulate herb, to 45 cm high. Plants frequently of several leafy shoots, with 2–5 leaves each. Rhizome 0.8–1 cm in diameter, internodes ca. 0.5 cm. Leaf sheath herbaceous, minutely tomentose to subglabrous, green to greenish-purple, 5–19 cm long, frequently auriculate at the apex, disintegrating with age. Petiole absent or to 4.5 cm long, minutely tomentose. Pulvinus slightly swollen, puberulent above, 0.6–1.5 cm long. Leaf blade herbaceous, entire, obovate to broadly elliptic, occasionally suborbicular, margin and leaf surface undulate, apex rounded with a point, base acute to obtuse, 17–30 cm long and 12–17 cm wide; the upper surface dark green with an irregular yellow-green band about ¼ the leaf width along the midrib, glabrous except for the tomentose midrib, covered with minute papilli (appearing as depressions on dried specimens) giving it a velvety sheen; the lower surface similarly covered but the interspersed stomata giving it a more or less dull aspect, varying from light grey-green to dark purple in color, glabrous except minutely puberulent (14×) on midrib and major veins. Cataphylls of

FIGURE 1. *Calathea dressleri* H. Kennedy.—A. Habit (scale in cm).—B. Inflorescence.—C. Snapped and pollinated flower with detail of staminodes, stamen, style and stigma (note cup-shaped stigma).—D. Seeds and dehisced capsules (each showing two of the three sections).—E. Flower, entire (small scale divisions 1 mm).

leafy shoots 1–2, green tinged with purple to dark purple, linear to narrowly oblong, to 15 cm long, usually 6–10 cm long, subglabrous to minutely tomentose especially at the base. Scape arising directly from the rhizome, subglabrous to minutely tomentose, 5–23.5 cm long, green to purple-green, pink at junction with the inflorescence, subtended by to 4 lanceolate, purple subglabrous scale leaves, 2.6–9.5 cm long and 0.8–1.8 cm wide. Inflorescence lax, sub-globose, 3.3–5.5 cm long and 3.2–5(–6) cm wide. After flowering the peduncle bends at the base, reflexing the inflorescence to the ground. Bracts 14–17, occasionally more, herbaceous, whorled, spreading and reflexed at the apex, ovate to elliptical, 2.45–3.5 cm high and 1.5–2.7 cm wide, apex obtuse, slightly pubescent on the abaxial surface; adaxial surface pure white with or without green markings on the margins or tinged light purple, abaxial surface pale purple-pink at base fading toward tip or uniformly pink-purple; each subtending 3 flower pairs; the latter provided with an indurate claviculate bracteole to 1.9 cm long. Prophyll bicarinate, membranous 2.0 cm long, oval, acute, glabrous to subglabrous. Flower opening spontaneously. Sepals narrowly ovate-linear, acute, hyaline, white, persistent in fruit, 19 mm long and 2.3–3 mm wide. Corolla tube white, glabrous, ca. 23 mm long; petals ovate, acute to obtuse, 0.9–1.3 cm long and 4.5–5.3 mm wide. Outer staminode white to pale purple, broadly ovoid to orbicular, clawed at the base, emarginate, 9 mm long and 6 mm wide. Callose staminode spatulate, tinged purple at the apex, petaloid, 1 cm long and 0.8 cm wide. Cucullate staminode ca. 7 mm long and 4–4.5 mm wide, purple at the apex provided with a filiform appendage 2–2.3 mm wide; anther 2 mm long. Ovary white, glabrous, 1.3–1.7 mm long. Stigma and style white. Capsule thin, white, with fleshy, raised apical rim and crowned by a withered persistent calyx, 9–10 nm high and 7 mm wide. Seeds 3 per capsule, trigonous, rugose on the outer surface, pinkish-brown, 4.5–5 mm long and 4 mm wide, provided with a white basal aril, 2–2.5 mm high.

PANAMÁ. PANAMÁ PROVINCE: La Eneida, region of Cerro Jefe, 750 m elevation, 8 July 1969, *H. Kennedy, R. L. Dressler & N. H. Williams 300* (COL, DAV); 13 September 1970, *H. Kennedy 500* (NY, PMA); woods around La Eneida, 5 August 1970, *J. Luteyn & H. Kennedy 1759* (DUKE); La Eneida, region of Cerro Jefe, 750 m, 11 August 1971, *H. Kennedy, R. L. Dressler & H. Wiehler 1111* (holotype MO; isotypes DAV, F, GH, K, US).

Flowering June to October. The population was growing on the steep banks above a stream. Though this was the only location observed, it may occur scattered throughout the cordillera toward Colombia. The plant was observed to be pollinated by *Euglossa nigrosignata* Moure at the type locality. It is quite distinct from any other known Panamanian *Calathea* in having the scape arise directly from the rhizome, patent to recurved white, herbaceous bracts, and undulate, beautifully marked leaves.

This species is named in honor of Dr. Robert L. Dressler, who first discovered it and made possible my collections of it and several other new species and whose assistance has been invaluable to my research.

Calathea venusta H. Kennedy, sp. nov.—FIGURE 2.

Planta modice robusta ad 1.43 m alta. Folia breviter (ad 1.9 cm) petiolata, petiolus tota longitudine callosus teres supra puberulus, plus minus inaequilatera anguste elliptica acuminata basi inaequilatera acuta mediano supra minutissime puberula ceterum utrinque glabra

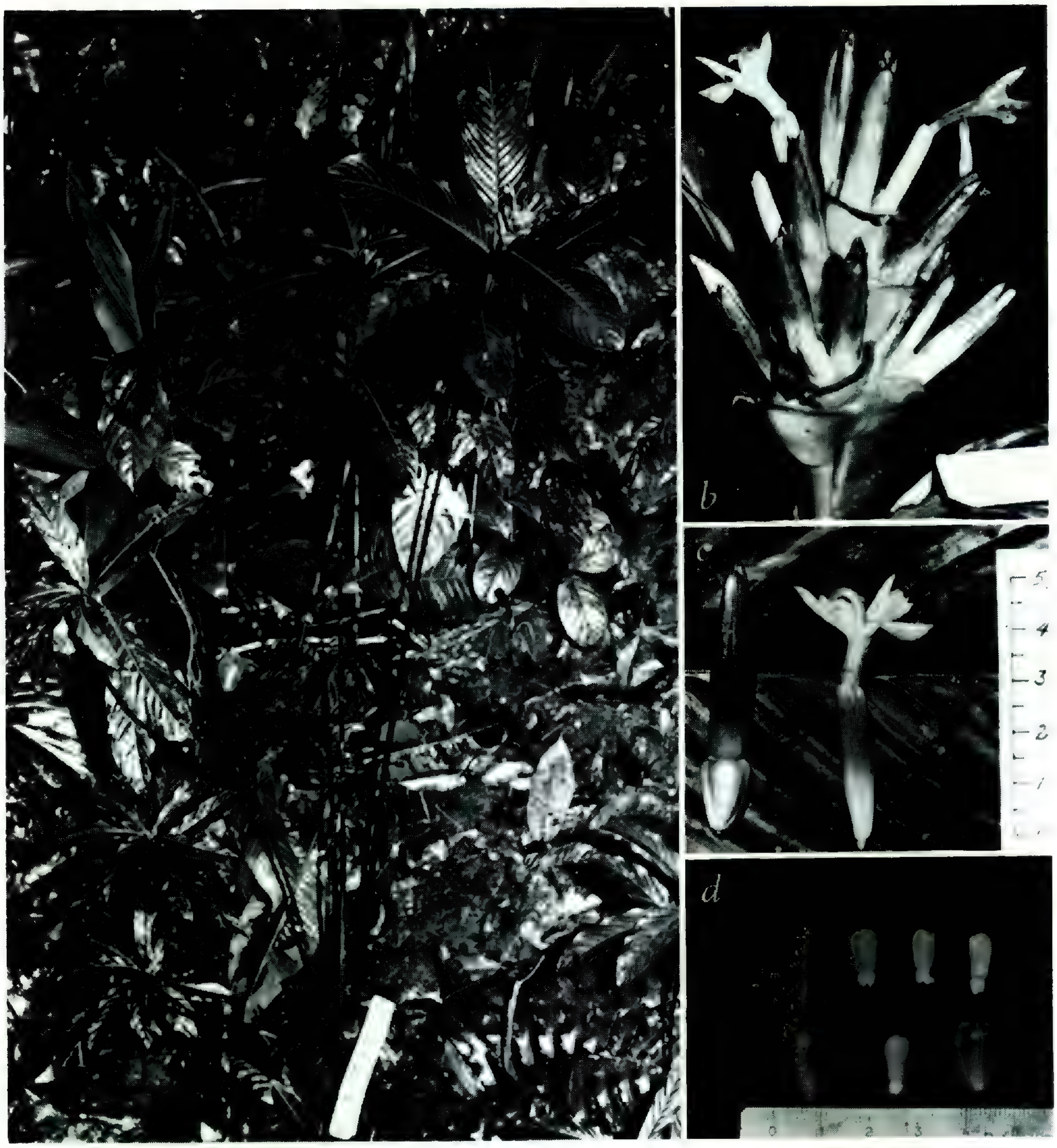

FIGURE 2. *Calathea venusta* H. Kennedy (scale in cm).—A. Habit, note clustered spiral leaves on both flowering and juvenile plants.—B. Inflorescence, note difference between sepals persistent on capsule and those of flower.—C. Snapped flower and capsule with persistent calyx (on leaf), note tridentate outer staminode.—D. Capsule with persistent calyx, dehisced capsule and seeds.

herbacea ad 34 cm longa et ad 10.5 cm lata; vagina virida super puberula ceterum utrinque glabra. Spica cum floribus ad 8 cm longa cylindrica vel subovoidea complanata folio comitata pedunculo gracili ad 17 cm longo sustenta; bracteae paucae ad 11 spiraliter dispositae ad 3 cm altae subreniformae vel depresse ovatae obtusae cum acumin subcoriaceae glabrae smaragdinae; paria florum ultra 6 mesophyllis et bracteolis membranaceis comitata; ovarium glabrum; sepala anguste oblongo-elliptica ad 3.25 cm longa; corollae tubus albus ad 4 cm longus lobi anguste oblongo-elliptici ad 1.6 cm mentientes; staminodium exteris obtriangularum tridentatum; callosum rectangularum ad 1.1 cm longum; cucullatum 9 mm longum. Capsula ovoidea ad 1.5 cm alta calyce demum coronata; semina rugosa trigona schistacea ad 1.05 cm alta, arillo albo munita.

Cauline herb 1.14–1.43 m high. Rhizome to 1.9 cm in diameter. Juveniles and subadults bearing 9–17 leaves, the uppermost of which are markedly reduced in size; the adult plant bearing 5–7 closely clustered cauline leaves supported upon an elongate stem internode, 0.9–1.01 m long. Leaves arising as distichous pairs but arranged spirally through twisting of the stem. Cataphylls (1–)2–3, narrowly ovate to linear-ovate, obtuse to acute, mucronulate, glabrous, occasionally outer 1 or 2 subglabrous with microscopic (14×) hairs, dark green or clouded green-purple; shiny green, glabrous within, thin, pliable, membranaceous above, basal portion fleshier, semi-coriaceous, remaining alive and green throughout flowering, 7–40 cm long, the innermost one 31–40 cm long. Stem olive green, drab, darker at base, lighter above, dark green-purple just below node, glabrous. Leaves 5–7 on flowering shoots, oblique, narrowly elliptical, apex acuminate, base unequal, acute, 23.2–34 cm long and 6.4–10.5 cm wide; the upper surface shiny deep grass green, midrib yellow-green, glabrous except for distal ½ of midrib puberulent, lower surface grey-green, opaque, glabrous, midrib yellow-green. Pulvinus olive green puberulent on upper side and at the basal junction with the leaf sheath, the rest glabrous, 0.6–1.9 cm long. Petiole absent or extremely rare. Leaf sheath stiff, parchment-like, center back hispid for to 8–10 cm, margins and rest of the leaf sheath glabrous, not auriculate, green, toward base dark greenish-purple, quite dark just above the node, 10.7–15 cm long in subtending leaf, others 14.5–23 cm long. Nodal area slightly swollen, yellow-green. Stem glabrous, rarely with microscopic hairs on the portion covered by the cataphylls, green to olive green, darkest at base. Inflorescence terminal, subtended by a foliage leaf, lax, cylindrical to subovoid, 6.8–8 cm high and 2.8–4.5 cm wide. Peduncle green, glabrous, 11.3–17 cm long. Bracts 8–11, spiral, spreading, apex patent to occasionally slightly recurved, subreniform to depressed ovate, apex obtuse with a point, semi-coriaceous, glabrous, shiny, grass green, apical portion turning dark purple with age, pale green, glabrous, within, 2.5–3 cm high and 4.3–5.8 cm wide; each subtending at least 6 flower pairs. Bicarinate prophyll rotund, membranaceous, translucent, yellow-green, tinged purple at apex with age, glabrous, ca. 2.4 cm long and ca. 2.4 cm wide. Mesophyll membranous, broadly elliptical, apex truncate, translucent yellow-green, glabrous, ca. 2.25 cm high and 1.9 cm broad. Bracteoles subtending individual flowers, membranous, glabrous, pale yellow-green, 2.3–2.4 cm long and 0.3–0.4 cm wide. Flower never opening spontaneously. Ovary cream-white, glabrous, 3 mm high. Sepals boat-shaped, narrowly oblong, obtuse, marginal edges inrolled, appearing acute. margins membranous, center and base semi-spongy, glabrous, basal ⅓ of sepal white, upper ⅔ chartreuse green, 3.1–3.25 cm long and 0.9–0.95 cm wide, living and persistent on capsule, becoming dark purple or green tinged with purple with age. Corolla tube white, glabrous, 3.8–4 cm long; corolla lobes unequal, narrowly oblong elliptic, obtuse, cream-white tinged faint yellow-green at apex, 1.5–1.6 cm long and 0.55–0.83 cm wide. Outer staminode obtriangular, tridentate, white, 1–1.1 cm long and ca. 0.6 cm wide. Callose staminode rectangular, apex truncate, irregularly bidentate, deep cream color, 1–1.1 cm long. Cucullate staminode cream colored at apex, golden to pale orange below, ca. 0.9 cm long and 0.5 cm wide, bearing a small, spoon-like appendage. Stamen cream to yellow-orange, bearing a reduced lateral

appendage to 1.5 mm wide, anther 3 mm long. Style and stigma golden. Capsule obovoid, smooth, thin, rounded at the apex, yellow-green to yellowish with tinge of purple at the apex, 1.25–1.5 cm high and 0.95–1.05 cm wide, crowned by a purple to purple-green expanded live calyx, sepals oblong, 3.5–3.9 cm long and 1.2–1.3 cm wide. Seeds usually 3 per capsule, trigonous, slate grey, rugose on outer surface, 0.9–1.05 cm high and 0.5–0.6 cm wide, bearing a basal white aril 3–4 mm high.

PANAMÁ. COLÓN PROVINCE: Río Guanche, mature forest about 1.5 miles upstream from bridge, ca. 10 m elevation, 27 September 1971, *H. Kennedy 1158* (paratype K); 1 November 1971, *H. Kennedy 1234* (holotype MO; isotypes F, US).

Flowering September through December. This species was pollinated by *Eulaema speciosa* (Mocs.) at the type locality. It was first known solely from the type locality but has since been found at La Lola, near milla 28, Limón Province, Costa Rica. This species differs from other Panamanian and Costa Rican Calatheas in having clustered leaves terminating an elongate stem, in the few apically patent, green, glabrous bracts, and its virtually total glabrousness. It is most closely related to *Calathea donnell-smithii* K. Schum. and is distinguished from it by the patent to recurved bract margins, the spiral and very close arrangement of the leaves instead of distichous and more widely spaced leaf arrangement. This is not so closely related to Woodson's *Calathea foliosa*.

The name is derived from the Latin venustus, meaning graceful, lovely.

Calathea robinae H. Kennedy, sp. nov.—FIGURE 3.

Planta gracilis 30–59 cm alta caespitosa, radicibus filipendulis. Folia inequilatera, elliptica acuminata basi obliqua acuta vel obtusa utrinque villosa. Spica laxa subglobosa utrinque villosa; bracteae 5–12 spiraliter dispositae herbaceae, smaragdinae ovate vel anguste ellipticae subcaudatae; paria florum 6 vel ultra, bracteolis indurato-claviculatis; ovarium glabrum; corollae tubus luteus, lobi lutei; staminodium exterius suborbiculatum lutem; callosum simile. Capsula viridia.

Herb 30–59 cm tall. Rhizome poorly developed, 6–8 mm in diameter. Roots bearing tuber-like storage organs to 2 cm long and 1.0 cm in diameter. Individuals forming clumps of leafy shoots. Branch shoots arise from the axils of older leaves; the stem portion lying horizontally along the ground or ascending obliquely, rooting at the nodes, the leaves upright. Cataphylls narrowly oblong-ovate, mucronulate, chartaceous, purple mottled with green, villose, glabrous within, innermost ones to 14 cm long. Leaf blade herbaceous, elliptic, unequal, apex acuminate, slightly eccentric, base acute to to obtuse, ca. 90°, suboblique, every other lateral vein raised giving a shallowly pleated appearance, (8.7–)11.5–21.5 cm long and (3.1–)4.3–7.5 cm wide; the upper surface deep green, slightly glittering; the lower surface pale, almost whitish grey-green, lateral veins dark green, the midrib yellow-green. Leaf villose throughout, hairs erect, up to 5 mm long. Pulvinus light yellow-green, villose, 0.7–1.6 cm long. Petiole villose, green or purple mottled with pale green, (1.3–)6–16.8 cm long. Leaf sheath herbaceous, villose, commonly mottled purple occasionally mottled greenish-purple, the basal 2–3 cm thickened, fleshy, especially if lying along the ground and commonly pale purple to whitish, 9–18.7 cm long. Inflorescence terminal, arising basally with internodes much reduced lax, subglobose to turbinate, 2.2–4

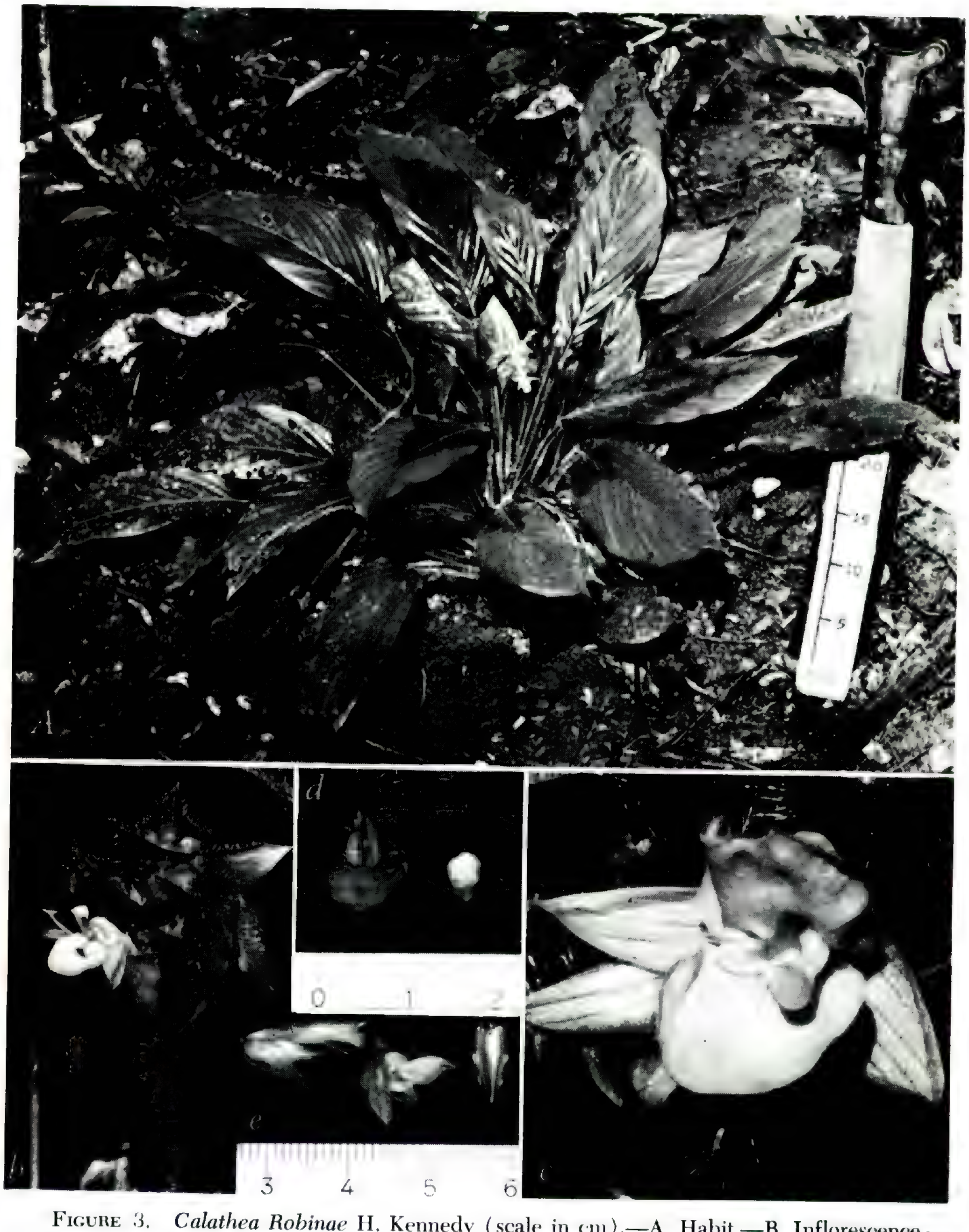

FIGURE 3. *Calathea Robinae* H. Kennedy (scale in cm).—A. Habit.—B. Inflorescence.—C. Open, unsnapped flower.—D. Capsule with persistent sepals and seed—E. Flower with mesophyll and claviculate bracteole attached, on the right, the bicarinate prophyll.

cm high and 3.5–4.5 cm in diameter (bract tip to bract tip) when living; after flowering, the peduncle frequently bends, reflexing the inflorescence to the ground. Peduncle villose, mottled purple and light green, (12–)18–30.6 cm long. Bracts 5–12, herbaceous, spirally arranged, spreading, apex elongated, patent to slightly recurved, 2.2–3.2 cm high and 1.1–2.7 cm wide. Lowermost bracts

(basally) transversely elliptic, the apex caudate to acuminate; the mid and upper bracts becoming ovate to elliptic or narrowly elliptic, acuminate to subcaudate, each subtending at least 6 flower pairs. The basal, imbricate, portion of the bract yellow-green, glabrous within; densely villose on abaxial surface and of thicker texture than the patent, apical portion. Apical portion of bract villose, deep green above; abaxial surface grey-green, veins dark green, very similar to leaves in color and texture. Bicarinate prophyll membraneous, broadly ovate, obtuse, translucent white at base, apex pale green, back and carina glabrous back occasionally sparsely villose towards apex, sides densely villose; glabrous within, 1–1.2 cm high and 0.9–1.05 cm wide. Tricarinate prophyll similar in color and pubescence. Mesophyll membranous, broadly ovate to triangular, apex acute to acuminate, translucent white at base, apical ¾ light green, outer surface densely short villose, glabrous within, 1–1.2 cm long and 0.8–0.85 cm wide. Bracteoles subtending individual flowers absent. Each flower pair subtended by an indurate claviculate bracteole, 1.2–1.6 cm long; the lower portion thin, flattened, translucent, white, apical ½ indurate, yellow, triangular in cross section. Flower opening spontaneously. Sepals herbaceous, narrowly elliptic, apex acute to subacuminate, villose, whitish opaque basally, apical ½–⅓ pale green, margins hyaline, 1.35–1.5 cm long and 0.4–0.45 cm wide. Tube glabrous, yellow, 1.55–1.65 cm long, the basal nectar reservoir enlarged, ca. 0.5 cm long. Petals subequal ovate to narrowly ovate, acute, bright yellow, 1–1.1 cm long and 0.45–0.55 cm wide. Outer staminode clawed at base, apical portion elliptic to suborbicular, apex rounded, bright yellow, 1–1.5 cm long and 0.75–1.05 cm wide. Callose staminode petaloid, base broadly clawed, apical portion transverse elliptic to suborbiculate, apex emarginate, bright yellow, 1.05–1.2 cm high and 0.8–1 cm wide. Cucullate staminode yellow 0.55–0.65 cm long and 0.4–0.45 cm wide; appendage relatively long, finger-like, ca. 2.2 mm long. Anther yellow ca. 1.5 mm long, filament yellow, with petaloid appendage to 1.5 mm wide, upper ¾ of anther free. Ovary glabrous, white, ca. 1.5 mm high. Capsule trigonal, fleshy, translucent green, glabrous with a raised rim apically, apical edge of each face tridentate to irregular. Seeds usually 3 per capsule, trigonous, convex, rugose on the outer surface, 4–4.5 mm high and ca. 4 mm broad, bearing a white basal aril to 2.5 mm high.

COSTA RICA: LIMÓN PROVINCE: Old forest about 2 miles from La Lola on the road to Siquirres, near stream bed, 26 February 1972, *H. Kennedy, R. Andrews & R. L. Dressler 1379* (holotype F; isotypes BM, COL, CR, DAV, DUKE, GH, K, MO, NY, U, US).

Flowering February and March. The plants were observed along the banks of the stream on the slopes at a fairly constant level above the stream bed. The mottling of the petioles, leaf sheathes, and other parts is due to the absence of purple pigment and apparent reduction of chlorophyll in the raised basal cells of the individual hairs. This plant is readily distinguished from other Costa Rican and Panamanian Calatheas through being villose throughout, possessing green herbaceous bracts, yellow flowers, claviculate bracteoles, glabrous ovary, and the absence of bracteoles subtending the individual flowers.

This species is named in honor of Dr. Robin Andrews on whose study site it was discovered and with whom the collection was made.

Calathea vinosa H. Kennedy, sp. nov.—Figure 4.

Planta robusta elata 1.3–2.3 m alta. Folia longe petiolata, oblonga vel lineari-oblonga obtusa cum acumin basi rotundata vel truncata supra metallica atrocyanea glabra subtus vinosa tomentosa, trichomae uncinatae. Spica late cylindrica vel subovata pedunculo vinoso; bracteae spiraliter dispositae, initia reniformae ceterum late ovato-trullate saepe eburnae velutinae recurvatae ceterum stramineae extus velutinae; bracteolis membranaceis summis puberulis prophyllis et mesophyllis puberulis; corollae tubus albidus, lobi eburni; staminodium callosum rectangularum. Capsula obovata straminea; semina schistacea.

Caulescent herb 1.3–2.3 m high. Shoots with 1–2 elongate internodes above ground, bearing 2–4 leaves. Cataphylls coriaceous, thicker and somewhat fleshy toward base, ovate to narrowly ovate-triangular, apex acute to obtuse, mucronulate, subglabrous to finely tomentose (both straight and retrorsely barbed hairs) at the apex and margins, abaxially red-purple, adaxially light green and glabrous; upper portions rotting away with age, innermost cataphyll 60–93 cm long. Leaf blade oblong to linear-oblong, occasionally narrowly ovate in smaller leaves, apex obtuse to rounded with a point, base rounded to truncate, junction of blade to pulvinus shortly acuminate, coriaceous, stiffer than pliable, 65–105 cm long and 17.5–38.7 cm wide. Leaf blade above glabrous, dark semi-metallic bluish-green, midrib puberulent, light yellow-green. Leaf surface below dark red-purple, densely tomentose with retrorsely barbed hairs, each hair arising from a swollen bulbous base. Pulvinus terete, glabrous except for row of hairs above, dark red-purple commonly concolorous, or petiole occasionally slightly darker or lighter, confluent with petiole and virtually of same diameter, (3–)5.5–15 cm long. Petiole glabrous to subglabrous with a few scattered hairs along upper surface, occasionally bearing a faint, shallow groove to 1.5 mm wide on the upper side, 0.9–57.5 cm long; petiole of the uppermost, subtending, leaf 0.9–29 cm long, others to 59 cm long. Leaf sheath not auriculate, centrally glabrous with the clasping margins moderately short pubescent with straight hairs, becoming especially dense at the apex, stiff semibrittle, dark red-purple; glabrous, whitish green within; sheath of uppermost subtending leaf 17–31.5 cm long, others 48–144 cm long. Base of the leaf sheath, node, and upper 2–3 cm of the internode puberulent. Inflorescence terminal, peduncle subtended by a foliage leaf. Peduncle minutely tomentose with straight hairs, dark red-purple, 10–19 cm long. Inflorescence lax, broadly cylindrical to slightly ovoid, 12–14(–16.8) cm high and 7–8.5 cm in diameter. Bracts spiral, first few reniform, apex obtuse, later bracts longer and narrower, broadly trullate-ovate to trullate-ovate, apex acute to acuminate, often slightly excentric, outer margin and apex recurved, occasionally patent in young inflorescences, coriaceous, 3.6–5.5 cm high and 4.3–6.6 cm broad. Basal portion of bract pale straw-colored, recurved apical margin ivory or faintly tinged greenish white; upper bracts often bearing slight streaks of purple adaxially at the apex, outer surface and recurved margin densely velvety pubescent, basal half of inner surface glabrous. Each bract subtending to six flower pairs. Bicarinate prophyll broad transversely elliptic, obtuse, membraneous, translucent pale yellowish-green, densely puberlent, glabrous within except apex and margins, (2.5–)2.6–2.9(–3.1) cm high. Mesophyll membraneous, translucent, white, subglabrous at base, upper half pale yellow-green, densely puberulent. Bracteole subtending individual flowers, membraneous,

FIGURE 4. *Calathea vinosa* H. Kennedy (scale in cm).—A. Habit.—B. Inflorescence, note closed flower, lower right, snapped flower above.—C. Flowers, closed at left; center showing style and outer staminode; rightmost flower note stamen attached to callose staminode; extreme right, callose staminode alone.—D. Capsule bearing enlarged persistent sepals and in center, seeds with basal aril.

puberulent at apex. Flower never opening spontaneously. Sepals oblong to narrowly obovate, apical margins infolded, appearing acute, pale yellow, glabrous, 3.55–3.9 cm long and (0.9–)1.05–1.3(–1.5) cm wide, about 0.5 cm wide at base. Corolla tube glabrous, white at base, cream-colored above, 4.2–4.5 cm long; petals oblong to subobovate, obtuse, glabrous, cream-colored, subequal, 1.6–1.75 cm long and 0.8–1.1 cm wide. Outer staminode narrowly obovate to obtriangular, bifid, apical half shallowly cupped, white, 1.1–1.3 cm long and 6–7.5 mm wide. Callose staminode rectangular, apex truncate, irregular, with a small point in the center, completely callose, pale golden, 1.15–1.25 cm high. Cucullate staminode cream-colored, 1.1–1.2 cm long and 0.5 cm wide, provided with an apical filiform appendage to 1.5 mm high. Stamen with lateral petaloid appendage to

1.5 mm wide extending to the tip of the anther; anther 4.5 mm long. Style and stigma golden. Ovary white, glabrous, 3.5–4.5 mm high and to 2.5 mm in diameter. Capsules thin, pale cream-yellow, glabrous, smooth, obovoid, ca. 1.7 cm high and up to 0.9 cm wide, crowned by a persistent, enlarged calyx; sepals up to 1.45 cm wide at base. Seeds usually 3 per capsule, trigonous, rugose on outer surface, slate grey, 9–9.5 mm high and 4.5–5 mm in diameter, bearing a basal white aril to 3.5 mm high.

COSTA RICA: PUNTARENAS PROVINCE: Between Palmar Norte and Puerto Cortez, altitude 50 m, 6 August 1965, *A. Jimenez M. 2240* (F); Osa peninsula 8 km S of Rincon in swamp forest, 28 February 1965, *A. Jimenez M. 3024* (F); cultivated at Finca Las Cruces, property of Robt. Wilson, Las Cruces, 5–6 km S of San Vito de Java, from rhizomes collected in the forest NE of the Tropical Science Center field station, ca. 50 m elevation, 5 km W of Rincon de Osa; 8°42′ N, 83°31′ W; 23 September 1969, *H. Kennedy 384* (holotype F; isotypes COL, MO, US); Golfito, watershed forest, elevation ca. 20 m, 17 October 1970, *H. Kennedy 644* (DAV).

Flowering July to October. This species is pollinated at the type locality (Osa Peninsula) and adjacent Golfito area by *Euglossa asarophora* Moure. This species differs strikingly from other Costa Rican and Panamanian Marantaceae in that the under leaf, pulvinus, petiole and stem portions of the plant are dark red-purple, the undersurface of the leaf blade is covered with retrorsely barbed, hook-like hairs and in possessing appressed pilose cream to faint greenish recurved bracts.

The specific epithet vinosa refers to the dark burgundy color of the lower leaf surface and stem portions.

Calathea donnell-smithii K. Schum., Pflanzenreich IV. 48: 75. 1902.

Calathea picta sensu Woodson, Ann. Missouri Bot. Gard. 29: 334. 1942, *non* Hook. f.

This species was treated as *Calathea picta* by Woodson (1942). Plants collected at Cerro Campana, Panamá Province, Panamá, agree very well with photographs of the type of *C. donnell-smithii* and with plants collected in Costa Rica from an area cited by Schumann in the original description. These plants differ from *C. picta* in having no basal leaves, in bearing 4–6 leaves above the elongate stem internode instead of 2, in the presence of imbricate, glabrous, green bracts instead of semi-lax, straw-colored, velvety pubescent bracts with recurved margins, and in the plain green leaves instead of having a dark and light green color pattern above with dark purple below. *Calathea picta* Hook. f. is a synonym of *Calathea warscewiczii* (Math.) Koern., Gartenflora 7: 87. 1858.

Calathea latifolia (Willd. *ex* Link) Klotzsch *in* R. Schomburgk, Reisen Brit.—Guiana 3: 918. 1848.

Alpinia latifolia Willd. *ex* Link, Jahresber. 1(3): 22. 1820.
Thalia latifolia Link *ex* Roemer & Schultes, Mantissa 1: 10. 1822.
Calathea allouia var. *violacea* (Roscoe) Woodson, Ann. Missouri Bot. Gard. 29: 332, 1942, *sensu* Woodson, *non Phrynium violaceum* Roscoe.
Calathea violacea var. *hirsuta* Petersen, Fl. Bras. 3(3): 1890.

The combination *Calathea allouia* (Aubl.) Lindl. var. *violacea* (Roscoe) Woods. was intended for this species, but it was based on the Brazilian *Phrynium violaceum* Roscoe from Rio de Janeiro and must remain in the synonymy of that

species. I have compared living plants from Rio de Janeiro, Brazil, and Panama with Lindley's description of *Calathea violacea*, and the description clearly fits the Brazilian plant rather than the very different Panamanian plant. Specimens of each were sent to Kew for comparison with the Lindley material, and the identity of the Brazilian specimen was confirmed as *Calathea violacea* (Roscoe) Lindley. *Maranta clavata* Vell. and *Phrynium floribundum* Lem., which are both Brazilian and were listed by Woodson and Schery (1945) as synonyms of his variety *violacea*, are quite unlike the Panamanian plant, whatever their identity. This species, (*C. latifolia*) has also been confused with *Calathea allouia* (Aubl.) Lindl., which was first described as *Maranta allouia* by Aublet in 1775 and occurs in the West Indies and French Guiana. This plant is quite different from the above described species, the bracts of the two differing widely in form. The following species listed under *Calathea allouia* in the *Flora of Panama* (Woodson & Schery, 1945: 86) are not properly synonyms of either *C. allouia* or *C. latifolia*: *C. cylindrica* (Rosc.) Schum., *C. grandifolia* Lindl. and *C. macrosepala* Schum. Of the above species, only *Calathea macrosepala* occurs in Central America. Woodson's "pale yellow variety" (Woodson & Schery, 1942) is neither this species nor *C. macrosepala* Schum. but *C. marantifolia* Standl. which occasionally occurs sympatrically with *C. latifolia*. Experimental crosses have shown *C. marantifolia* and *C. latifolia* to be incompatible. Infrequently in Panamá, a form of *C. latifolia* with cream colored flowers is found in which the bracts are wholly green, sepals, petals and outer staminode are cream white. The cream colored flower is common in Colombia, Venezuela, and Trinidad but usually associated there with purple bracts. It is the cream flowered form which is confused with *C. marantifolia*.

Calathea marantifolia Standl., Jour. Washington Acad. Sci. 17: 250. 1927.

Calathea lagunae Woods., Ann. Missouri Bot. Gard. 29: 333. 1942.
Calathea allouia (Aubl.) Lindl., *sensu* Woodson (1942), *non* Aublet.

The type is an unusually small individual of the species but otherwise agrees with larger individuals collected by Standley and Valerio in the same area and at the same time. Standley (1937) states it "may be only a reduced form of *C. macrosepala* Schum." It is not, however, a form of *C. macrosepala* but a distinct species with a wide range and a concomitant amount of variation. This species has been frequently confused with *C. macrosepala* Schum. (in Standley, 1931, 1937) and with *C. latifolia* (Willd. *ex* Link) Klotzsch (in Woodson & Schery, 1945). *Calathea marantifolia* differs from these species in the structure of the leaf and in details of the capsule. Both *C. latifolia* and *C. macrosepala* die back to the rhizome during the dry season, while *C. marantifolia* is found in much wetter habitats and retains its leaves in the dry season.

Calathea leucostachya Hook. f., Bot Mag. *Pl. 6205*. 1875.

Calathea valeriana Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 190. 1937.

This species is reported for Costa Rica by Standley (1937) and recently has been found also in the Atlantic lowlands of Panamá.

PANAMÁ. COLÓN PROVINCE: Rio Guanche, ca. 1.5 miles upstream from the bridge, 17 July 1971, *H. Kennedy, R. Foster & R. L. Dressler 1157* (DAV).

Calathea leucostachya as pictured in Hooker's *Botanical Magazine* appears identical with plants collected near San Ramon, Costa Rica, close to the type locality of *C. valeriana*. The Panamanian plants differ in having the underside of the leaf pubescent rather than glabrous. This plant is very distinctive in its habit, pubescence and form of inflorescence.

Calathea cleistantha Standl., Jour. Washington Acad. Sci. 17: 250. 1927.

This species was previously reported only from Costa Rica near Guapiles. Specimens collected near La Mesa, in Coclé Province, agree well with material of this species collected at La Lola (near mile 28) Limón Province, Costa Rica, close to the type locality.

PANAMÁ. COCLÉ PROVINCE: El Valle de Antón, La Mesa, elevation ca. 800 m, 1 April 1973, *H. Kennedy, A. Kennedy & E. Kennedy 3030* (MO).

This species is very distinctive in having the inflorescences arise from the rhizome at ground level and the unusually long petals and outer staminode.

Hylaeanthe panamaensis (Standley) H. Kennedy comb. nov.

Myrosma panamensis Standl. Jour. Washington Acad. Sci. 15: 4. 1925.

This distinctive genus was described by Jonker-Verhoef and Jonker (1955: 175) and included four additional species, one of which, *H. hoffmannii* (Schum.) Jonk. & Jonk., occurs in Costa Rica. This species was not mentioned by Jonker-Verhoef and Jonker, but agrees in all respects with *Hylaeanthe*.

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CALDERONELLA, A NEW GENUS OF GRASSES, AND ITS RELATIONSHIPS TO THE CENTOSTECOID GENERA[1]

THOMAS R. SODERSTROM[2] AND HENRY F. DECKER[3]

ABSTRACT

A new genus and species, *Calderonella sylvatica* (Gramineae), is described from the rain forests of Panama. Features of its spikelet morphology and leaf anatomy reveal that the affinities of *Calderonella* are with the centostecoid group of grasses, of which *Zeugites* appears to be the most closely related genus. A brief characterization of the centostecoid group is presented, as well as a key to the genera included in it, with comments on each.

In the rain forests of tropical America occur some of the most ornamental members of the grass family. The new genus is no exception. Delicate plants which inhabit the densely shaded forests of Panama (Fig. 1) in the Province of Colón, the lanceolate blades and white spikelets borne on long filiform culms create the illusion of a liliaceous plant (Figs. 2–3). Plants of *Calderonella* are common in the forests of Santa Rita and were first discovered by Correa and Dressler in January 1968, when access to the previously undisturbed forests was made possible by a new lumber road. Large gatherings have since been made in the same location, with field observations carried out by Cleofé E. Calderón, after whom the genus is named. The specific name alludes to the forest habitat of the new grass.

Plants of the new genus also occur in the forests of Cerro Jefe, Provincia de Panamá. Living material was collected by Calderón in October 1971 and is now under greenhouse cultivation in Washington, D.C.

Calderonella sylvatica Soderstrom & Decker, gen. et sp. nov.—Fig. 5.

Gramen perennis usque ad 30 cm altis. Culmi erecti vel suberecti, filiforme, compresses. Foliorum vaginae compressae, forte nervatae, tessellatae; ligula membranacea, brevis, fusca, chartacea; lamina lanceolata pagina abaxiali transverse nervata, petiolo basi solido, piloso, geniculato. Inflorescentia angusta, racemiformis, spiculis 6 vel 7. Spiculae flosculis 3–5, infimo femineo, supernis masculis, gluma inferiore 15- vel 16-nervata, tessellata, glume superiore 10- vel 11-nervata, tessellata. Flosculus femineus ad maturitatem gibbosus, lemmate 15–19-nervato, tessellato. Flosculi masculi non gibbosi, lemmate 5–9-nervato, tessellato. Lodiculae 2, carnosae, multi-nervatae, irregulariter obtusae. Stamina 3. Ovarium globosum, stylo brevi, stigmatibus 2. Caryopsis lateraliter compressa. Embryon parvus. Hilum rotundatum basale.

Perennial to 30 cm high (excluding the inflorescences) in clumps of several shoots clustered together in cespitose-like arrangements, the shoots arising from approximate nodes of a rhizome with foreshortened internodes, or internodes absent, the internodes between the cespitose-like clusters elongated into stolons. Culms erect or suberect, filiform, compressed, glabrous, the elongated portion

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[1] We thank Dr. Cleofé E. Calderón for her review and constructive criticism of the manuscript.

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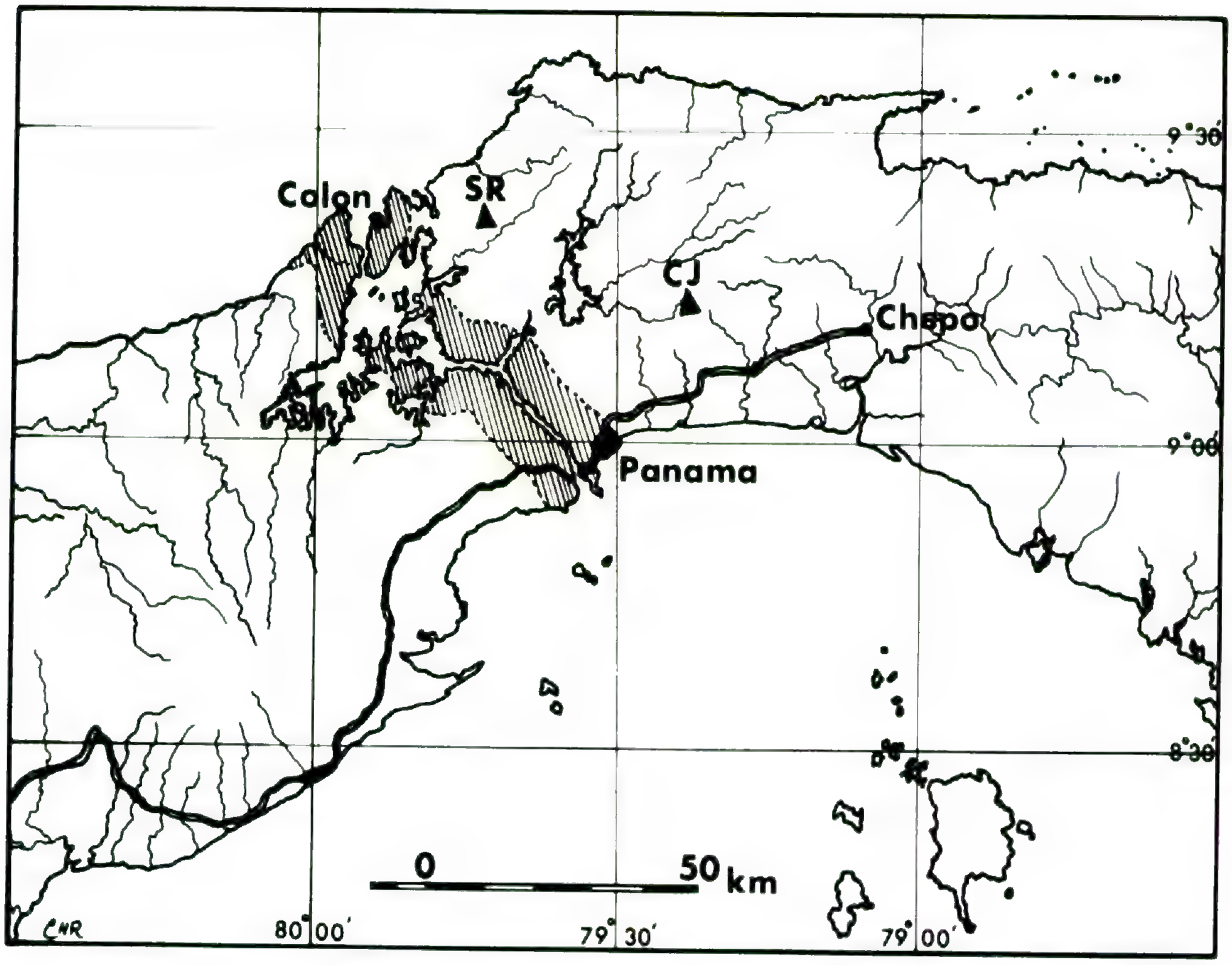

FIGURE 1. Map of Panama showing localities in which *Calderonella sylvatica* has been collected. SR, Santa Rita; CJ, Cerro Jefe. The cross-hatched area is the Canal Zone.

which terminates in the inflorescence with a single node at which is borne a sheath 7–8 cm long bearing a reduced blade. Flowering culm at maturity geniculating at the node and assuming a more or less horizontal position at time of spikelet abscission. Leaf sheaths compressed and strongly nerved with transverse veinlets, especially in the upper part, green over the back, golden-brown on the thinner margins, glabrous; ligule a brown chartaceous membrane 0.1–0.2 mm long, pilose abaxially; blades attenuate basally into a petiole 2–8 cm long, the lowermost 1–2 mm of which is thickened, solid, densely pilose, geniculate, the upper expanded portion of the blade lanceolate, tapering evenly at both ends, 8–20 cm long, 1–1.5 cm wide, flat, glabrous on the abaxial surface, sparsely papillose-strigose on the adaxial surface (at least when young), the midvein white, forming a prominent ridge on the abaxial surface, the veins connected by numerous transverse veinlets manifest on the abaxial surface only. Inflorescence a raceme 3–5 cm long consisting of 6 or 7 evenly spaced spikelets with thick pedicels 1–2 mm long, on the terminal portion of a weak, filiform peduncle

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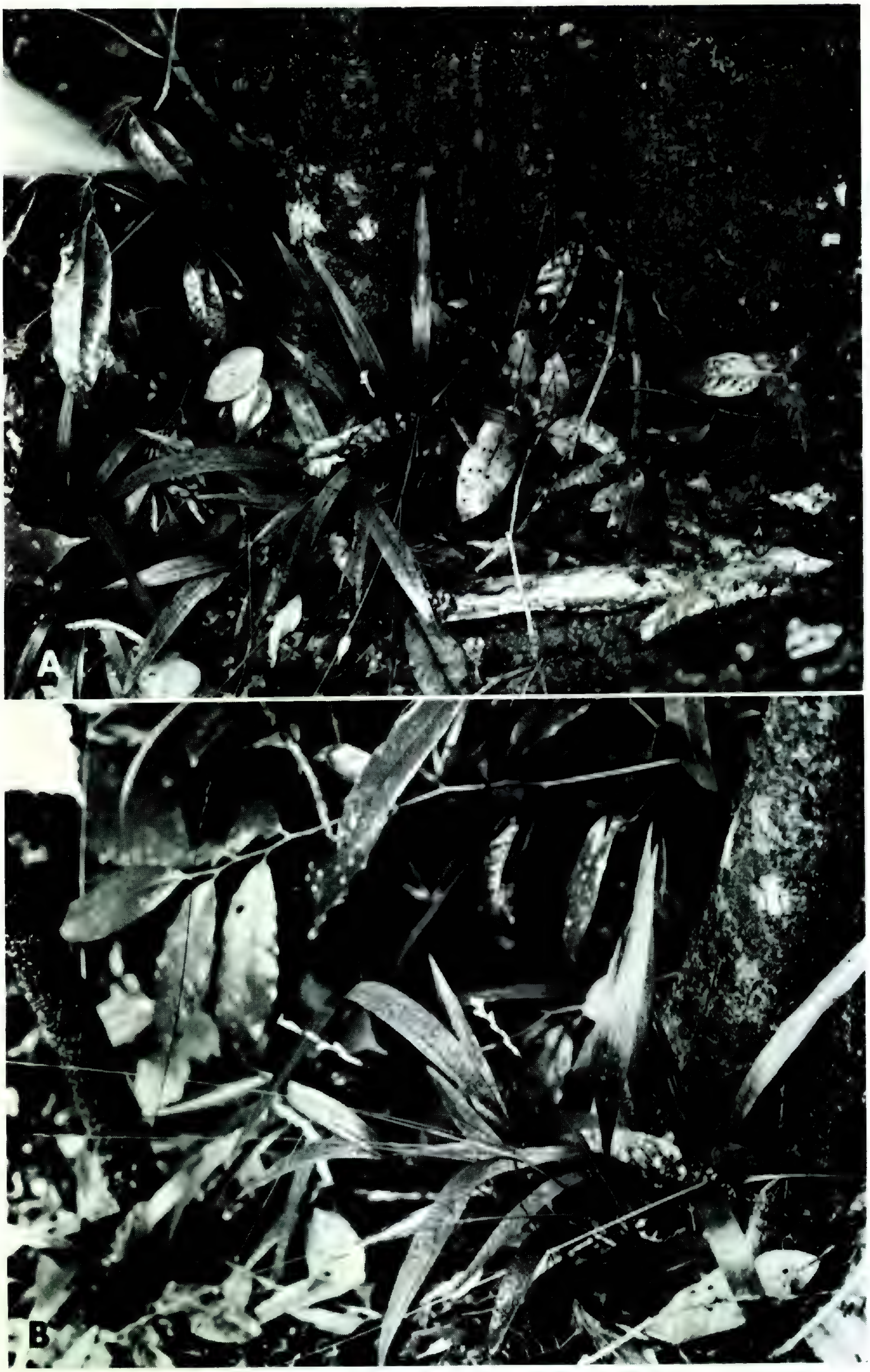
FIGURE 2. Photographs of *Calderonella sylvatica* in the field (Santa Rita forest, Panama, *Calderón 2141*).—A. Mature plant growing at base of tree.—B. Close-up of basal part of plant.


A
B

to 30 cm long. The uppermost spikelet developing first, at maturity ca. 8 mm long, stramineous when young, testaceous at maturity, with 3–5 dimorphous florets, the lowermost pistillate (and maturing first), the remaining staminate (or the one succeeding the pistillate with a pistil in addition to the stamens but not producing fruit?), at first lanceolate and parallel to the rachis, at maturity the lowermost floret becoming gibbous and causing the whole spikelet to bend at right angles to the rachis and become triangular in appearance. Disarticulation of the spikelets below the glumes. Lower glume ca. 6.5 mm long, lanceolate with thick pronounced veins, sparsely papillose-pilose between the nerves (evident especially at maturity), ciliolate on the upper margin, 15- or 16-nerved (1 or 2 of which may be faint and manifest only at the base) with numerous transverse veinlets (especially in the upper two-thirds), the basal margins encircling the rachilla and enclosing the base of the upper glume; upper glume ca. 4.5–5 mm long, parabolical (from side view), with the thick pronounced veins, sparsely papillose-pilose between the veins (evident especially at maturity), ciliolate on the upper margin, 10- or 11-nerved (of which one nerve may be faint and visible only at the base), with a few transverse veinlets on the upper half, the margins fuse at the very base and encircling the rachilla. Lower floret pistillate (with three staminodes present), at first erect and lanceolate, at length becoming gibbous and turned 90° from the rachilla; lemma ca. 5 mm long, bowed out at the base, sparsely papillose-pilose between the thickened nerves (evident especially at maturity), 15–19-nerved (many nerves manifest only at the base), with several transverse veinlets on the upper half of the margins encircling the rachilla at the base and fused on the lower one-eighth of the length; palea shorter than the lemma, with two keels, each keel with a nerve and wing extending from each keel, the two nerves connected at the summit by a transverse veinlet, narrowed abruptly above the truncate ciliolate apex, otherwise glabrous. Upper florets staminate, ca. 2.2–3.5 mm long; lemma 2.7 mm long, lanceolate, glabrous, membranous, 5–9-nerved with the nerves near the midvein connected toward the summit by a transverse veinlet, the margins at the base encircling the rachilla; palea with 2 keels, each containing a single nerve, winged. Lodicules of the lowermost floret 2, opposite the palea, 0.5–1.2 mm long, cuneate, broad, fleshy throughout with the outer margin a little higher than the inner, and with 3 or 4 vascular traces extending almost to the apex, the inner edges somewhat overlapping in front of the ovary at its base and partially fused below. Androecium consisting of 3 stamens, the filaments attached to the connective toward the base of the anther. Mature gynoecium consisting of a roundish ovary which narrows apically into a short style about 0.2 mm long, bifurcating to produce two branches, each ca. 6 mm long, the lower two-thirds glabrous, the upper third covered with short stigmatic processes. Caryopsis 2.3 mm long, compressed laterally, ventrally,

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FIGURE 3. Photographs of *Calderonella sylvatica* in the field (Santa Rita forest, Panama, *Calderón 2141*).—A. Mature plant with many inflorescences.—B. Young inflorescence.—C. Inflorescence at a later stage showing the stigmas exserted from the uppermost spikelets, which develop first.

A
B
C

and at the base, with the base of the style persistent; embryo small; hilum basal, round.

Holotype: PANAMA. PROVINCIA DE COLÓN: Santa Rita lumber road, 24 May 1968, *R. L. Dressler 3511* (Holotype, US; isotypes, BAA, K, MO, P).

Additional specimens examined: PANAMA. PROVINCIA DE COLÓN: Santa Rita lumber road ca. 25 km before Colón on the Transisthmus highway, 5 March 1968, *Calderón 2079a* (BAA, K, P, US). Santa Rita, 12–20 km from the Transisthmus highway, elevation ca. 300 m, latitude 9°21′ N, longitude 79° 42′ W, shady forest, abundant, 31 October 1971, *Calderón & Dressler 2141* (B, BAA, CORD, F, K, MO, NY, OWU, P, RB, RM, S, TNS, US). East Santa Rita lumber road, 16 January 1968, *Correa & Dressler 643* (US). Santa Rita lumber road, ca. 15 km east of Colón forest, 5 October 1969, *Dressler & Lewis 3729* (MO).

LEAF ANATOMY

The mesophyll of *Calderonella* consists of a rather distinct *palisade layer*, 1 or 2 cells in height, while the remainder of the mesophyll consists of rather large, irregularly shaped chlorenchyma cells. The *bulliform* cells are arranged in prominent, often wide fans of 3–5 cells each on the adaxial side of the leaf. The bulliform cells are large, inflated, projecting on the adaxial epidermis and frequently extending to about half the width of the mesophyll. The vascular bundles are surrounded by a large-celled outer bundle sheath and an inner bundle sheath composed of much smaller cells widely thickened on their inner surfaces. The outer bundle sheath is complete and conspicuous on vascular bundles of all sizes except on the midvein, where it is obscure and grades into the parenchyma cells making up the enlarged portion of the midrib. Frequently the outer bundle sheath cells on the lateral sides of the vascular bundle are more prominent and extend into the mesophyll. The vascular bundles occur in approximately 2 sizes: small bundles and first order bundles in ratios varying from 5 to 8 small bundles to 1 first order bundle. The *sclerenchyma* is confined to small patches or girders immediately beneath the epidermis and above and below each vascular bundle. On first order bundles in particular, the sclerenchyma frequently extends from the epidermis to the outer bundle sheath but does not interrupt it. Wider, thicker plates of sclerenchyma occur in the midrib.

In the abaxial *leaf epidermis* dumbbell-shaped silica bodies are frequently in a single row over the veins. The silica bodies in the intercostal regions are cross-shaped and modified cross-shaped. The filiform bicellular microhairs are approximately 30 microns long with both the basal and distal cells approximately equal in length. The stomata are ovoid with low dome-shaped, sometimes triangular subsidiary cells, and are confined to 1 or 2 rows on each side of the veins. The fundamental cells of the epidermis have relatively thick, sinuous walls, are elongate, and are more or less 6-sided. The fundamental cells are separated by cross-shaped siliceous cells or microhairs.

HISTORICAL CONSIDERATIONS

Features of spikelet morphology and leaf anatomy reveal that the affinities of *Calderonella* are with the centostecoid ("centothecoid") group of grasses. Since various genera have been assigned to this group by different authors, and the history of the group indicates a number of changes in its disposition, we feel

that the following account is necessary before we define the group as we now understand it. The historical considerations will be followed by a brief characterization of the gross morphology of the group and its differentiation from the bambusoid group of grasses. We will then present a key to the genera included in the centostecoid group with brief comments on each genus.

Centosteca (Fig. 4a, b) and genera related to it have been recognized variously as a tribe (Centotheceae), subtribe (Centothecinae), or group (centothecoid). The genus *Centosteca* was described by Desvaux (1810: 189) based on *Cenchrus lappaceus* of Linnaeus. Two years later Palisot de Beauvois (1812: 69) published the name of *Centotheca*. Desvaux in the following year (1813: 70) employed Beauvois' spelling giving the source of derivation as Greek "χεντων, piquant, et θηχη, enveloppe." Sharp (piquant) covering (enveloppe) is doubtless in allusion to the uppermost lemma which is covered with reflexed bristles in the type species. In the 1810 publication Desvaux published two other generic names ending in "steca," namely *Heterosteca* (page 188) and *Calosteca* (page 189). In the 1813 publication he retained the name *Heterosteca* but changed *Calosteca* to *Calotheca* and *Centosteca* to *Centotheca*. Interestingly, for the derivation of *Centotheca* (1813: 70) he gives θηχη as "enveloppe"; for *Calotheca* (1813: 71) he gives θηχη "couverture"; and for *Heterosteca* (1813: 68) he also gives στεχη as "couverture." It is apparent that Desvaux considered both words "theca" and "steca" to be equivalent to "couverture" or covering, and this must have been his original thinking when he formulated the name *Centosteca*. Even though Palisot de Beauvois changed the spelling of *Centosteca* and Desvaux himself accepted this change, the original spelling must be retained as it was neither an orthographic nor typographic error (see Article 73, *International Code of Botanical Nomenclature*). In a recent note on the genus, Monod de Froideville (1971: 57) remarks that "the spelling [*Centotheca*] has been used by all authors . . . and it is obvious that it should be retained, although according to the *Code of International Botanical Nomenclature*, the original spelling should be used." The name *Centotheca* could be used only if conserved, but since the original spelling appears to be correct, representing neither an orthographic nor typographic error, we see no reason for its conservation.

The history of *Centosteca* and genera considered allied to it is interesting to recount, as the earlier authors were well aware of the relationships of many of these genera from their observations of gross morphology. Nees von Esenbeck (1829), in his work on Brazilian grasses, placed *Orthoclada* (Fig. 4c) in his tenth "family" of the order "Gramineae"—Gramineae Bambuseae. He considered it to be related to such bamboos as *Arundinaria* and *Merostachus*, placing these three apart from the true bamboos, "Bambuseae verae." But Steudel (1855: 116) considered *Centotheca* to be related to *Panicum* and placed it in Tribe III, Paniceae. However, most authors since his time have considered the genus to be a member of the Festuceae. In his magnificent treatise on grasses, Bentham (1881) recognized the Centotheceae as the seventh subtribe of the Festuceae, remarking that the tribe is formed of small tropical grasses, several of which had been referred to Bambuseae but rejected from that group by specialists. He mentioned that even though the spikelets resemble some Eu-Festuceae or Meli-

A
B
C

ceae, the foliage is unusual in the broad flat lamina which has cross venation, a feature which is not found elsewhere in the order except in a few Bambuseae. Bentham included five genera in the subtribe Centotheceae: *Centotheca* (mentioning here also *Poa mucronata* [= *Megastachya*]), *Orthoclada*, *Lophatherum*, *Streptogyne* [*Streptogyna*], adding that this genus is quite isolated in habit and in a number of characters, and *Zeugites*. The same treatment was given by Bentham and Hooker in *Genera Plantarum* (1883: 1092) and also by Hackel, in Engler and Prantl, *Die natürlichen Pflanzenfamilien* (1887: 71) except for the addition of *Poecilostachys* Hackel.

Evidently the first to consider the group as a tribe was Ridley (1907), who included *Centotheca* and *Lophatherum* in the Centotheceae in his treatment of Malaysian grasses. Bews (1929) in his treatment of the world's grasses included *Centotheca* (which he considered the most primitive of the group), *Zeugites*, *Lophatherum*, and *Streptogyna* in the subtribe Centothecinae of the Festuceae. Hubbard (1934) followed Bews in recognizing the Centothecinae as a subtribe of the Festuceae, and included *Centotheca*, *Orthoclada*, *Lophatherum*, and *Zeugites*. He did not include *Streptogyna* nor did he make mention of the genus elsewhere in his treatment of the Gramineae. Prat (1935), basing his conclusions on studies of the leaf epidermis and other microcharacters, pointed out that *Centotheca* and allies were quite unlike *Festuca* and related genera, *i.e.* not "festucoid." He stated that the tribes "Pappophorinées" and "Centothecinées" are quite different from festucoid grasses and further remarked that the world-wide distribution of the genera of the latter favored an ancient distribution. In the tribe he recognized *Centotheca*, *Zeugites*, *Lophatherum*, and *Streptogyna*. Roshevitz (1937) recognized the same tribe in his series Phragmitiformes and to the genera listed by Prat added *Bromuniola* and *Pseudostreptogyne*. Hubbard (1940), in his description of a new species of *Orthoclada* from Africa, recognized the tribe Centotheceae as had Ridley and Prat before him.

On the basis of morphological studies the above authors, at one time or another, indicated a close relationship among the following genera: *Bromuniola*, *Centosteca*, *Lophatherum*, *Megastachya*, *Orthoclada*, *Poecilostachys*, *Pseudostreptogyne*, *Streptogyna*, and *Zeugites*. One of these, *Poecilostachys*, a genus of Madagascar, has spikelets which are panicoid and is most closely related to the panicoid genus *Oplismenus*, according to Stapf (1916). The systematic position of another Malagasy genus, *Pseudostreptogyne*, has been discussed by Hubbard (1936). The type of the genus, *P. richardii* A. Camus, was found to be synonymous with *Streblochaete longiaristum* (A. Rich.) Pilger, a grass whose relationship is with *Danthonia* and *Phaenanthoecium*. The systematic position of *Streblochaete* has been discussed by Tateoka (1969), who also noted (1958) that the leaf anatomy of *Streptogyna* agrees with that of bamboos; he further indicated that the three lodicules of *Streptogyna* were similar to those of bamboos.

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FIGURE 4. Field photographs of Old and New World genera of the centostecoid group.—A.–B. *Centosteca lappacea* (Purwodadi, Java, Indonesia, *T. R. Soderstrom & Soejatmi Sunarko 1360*).—C. *Orthoclada laxa* (Madre de Dios, Costa Rica, *C. E. Calderón 2110*).

FIGURE 5. Habit sketch and spikelet dissection of *Calderonella sylvatica*.—A. Spikelet, ×6.—B. Pistil of young flower, ×12.5.—C. Lower glume, ×6.—D. Upper glume, ×6.—E. Male florets, ×6.—F. Stamens, with lodicules at the base, ×12.5.—G. Lemma of female floret, ×6.—H–I. Lodicules, ×25.—J. Caryopsis, side view, ×6.—K. Caryopsis, front view, ×6.—L. Habit of the plant, ×0.5.—M. Section of leaf to show cross veins, greatly enlarged.—N. Juncture of leaf sheath and blade, ×1. (Drawing *b* based on *Calderón & Dressler 2141*, all others on *Dressler 3511*.)

Metcalfe (1960) also pointed out that the leaf anatomy of *Streptogyna* is like that of the bamboos, and recently Calderón and Soderstrom (1973) included the genus in the subfamily Bambusoideae.

Investigations made from standpoints other than gross morphology have shed light on the relationships of several of these grass genera and have also indicated that the following three belong to the *Centosteca* line: *Chasmanthium*, *Chevalierella*, and *Ramosia* (which we consider to be synonymous with *Centosteca*).

The Centostecoid Group

The following characterization of the group covers only features of the gross morphology. A comparative study of the leaf anatomy of all centostecoid genera is obviously needed before a complete delimitation of the group can be made.

Rhizomatous and/or stoloniferous annuals or perennials found in moist habitats of tropical and subtropical woodlands, ravines, or lake margins, or in warm temperate woodlands. *Leaves* typically petiolate with relatively broad blades and usually with manifest transverse veinlets; ligules membranous or ciliate or membranous with ciliate margins. *Spikelets* compressed laterally, 2–many-flowered with reduction either below or above the fertile florets, the florets perfect or unisexual; lodicules 2, more or less cuneate, many-nerved; stamens 1–3; stigmas 2; caryopsis flattened laterally; hilum basal, punctiform.

Genera included: *Bromuniola*, *Calderonella*, *Centosteca*, *Chasmanthium*, *Chevalierella*, *Lophatherum*, *Megastachya*, *Orthoclada*, and *Zeugites*.

Centostecoid and Bambusoid Grasses

Most of the grasses—in number of taxa and individuals—which are found in the shaded habitat of the tropical American forests are related to bamboos. Because they are herbaceous, unlike their woody relatives, they have been referred to as herbaceous bambusoid grasses (Soderstrom & Calderón, 1971).

The herbaceous bambusoid grasses which are found at Santa Rita, along with *Calderonella*, are such genera as *Cryptochola* and *Maclurolyra*, members of the tribe Olyreae (Calderón & Soderstrom, 1967, 1973). The petiolate blades with tessellate venation and shaded habitat might lead one to assume that the new genus is also an herbaceous bambusoid grass. Indeed, the historical account given above shows that centostecoid genera have more than once been assigned a relationship with bamboos. Although superficial resemblance may be responsible for this, the characters presented in Figure 6 can be used to distinguish grasses of the two groups.

In the centostecoid genera the cells of the outer bundle sheath are large and inflated; the bulliform cells are large, prominent, and fan-shaped; and the mesophyll is composed of a well-marked palisade layer and spongy parenchyma with fairly large intercellular spaces. In the bambusoid genera the cells of the outer sheath are not so prominent nor are the bulliform cells. The mesophyll, furthermore, consists of fusoid cells and arm cells, the latter arranged in layers parallel to the epidermis. Lodicules of centostecoid grasses are two in number, more or less truncate, and glabrous, while those of bambusoid grasses are three in number, usually pointed, and often with hairs. The caryopsis of centostecoid

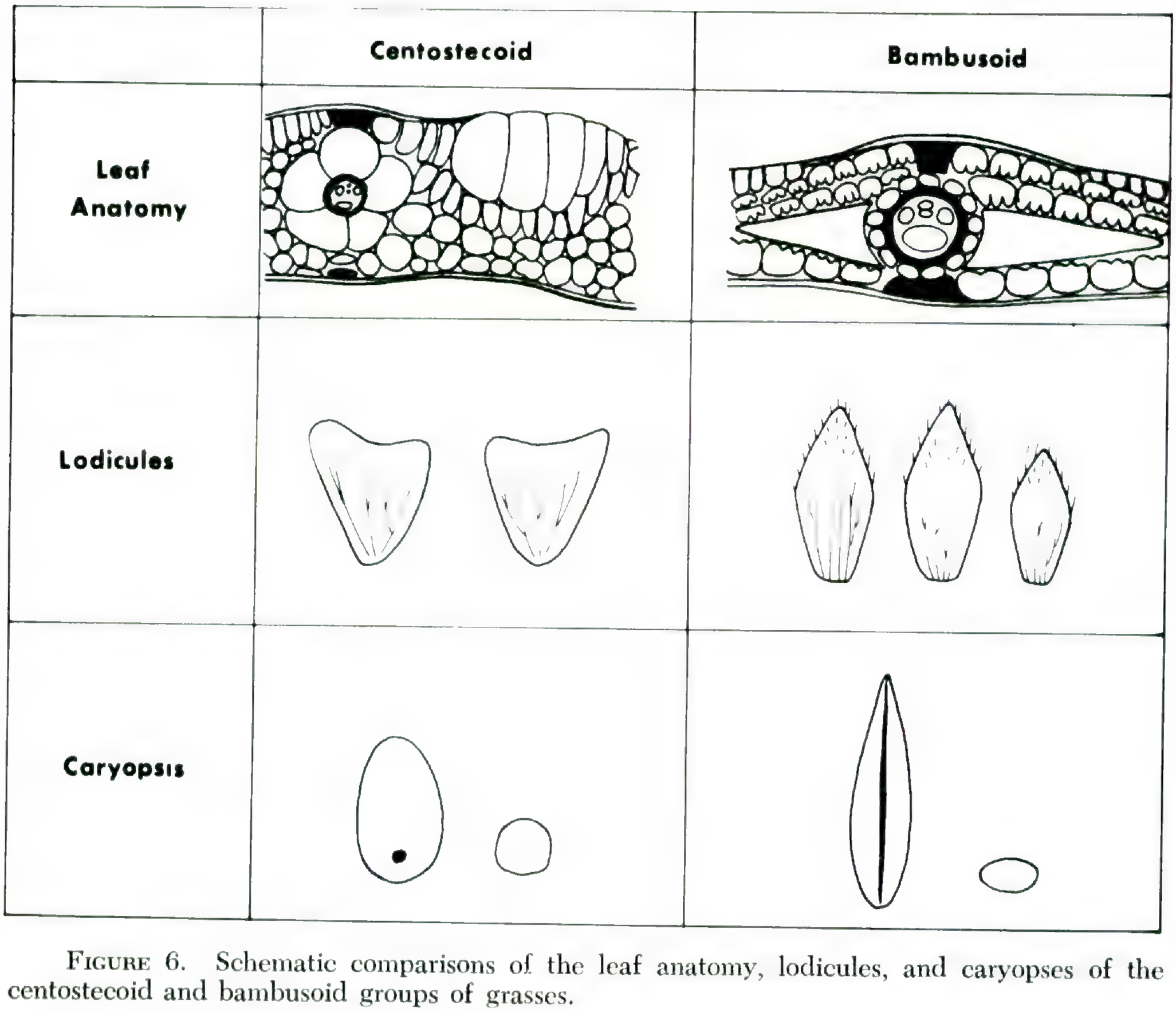

FIGURE 6. Schematic comparisons of the leaf anatomy, lodicules, and caryopses of the centostecoid and bambusoid groups of grasses.

grasses is compressed laterally and has a punctiform hilum, while in bambusoid grasses the caryopsis is usually round or dorsally compressed and has a linear hilum which extends almost the entire length of the caryopsis.

PROVISIONAL KEY TO THE GENERA OF THE CENTOSTECOID GRASSES

1. All florets within the same spikelet unisexual, the lowermost larger, ♀, becoming gibbous at maturity, upper florets ♂ 2
1. Florets, at least some, within the same spikelet bisexual; reduced florets also generally present 3
2. Inflorescence a panicle; fertile lemma less than 10-nerved; stigmatic processes long, thin (tropical America from Mexico and West Indies to Bolivia) ..... *Zeugites*
2. Inflorescence a raceme; fertile lemma more than 10-nerved; stigmatic processes short, thick (Panama) ..... *Calderonella*
3. Blades not manifestly tessellate (eastern and southern U.S.A. and northern Mexico) ..... *Chasmanthium*
3. Blades manifestly tessellate 4
4. Rachilla of uppermost (usually rudimentary) floret adnate (on the lower part) to the palea of the preceding floret (tropical America and Africa) ..... *Orthoclada*
4. Rachilla of uppermost floret free 5
5. Lemmas awnless or mucronate 6
5. Lemmas awned 7
6. Spikelets many(10–16)-flowered (Africa) ..... *Megastachya*
6. Spikelets few (1–3)-flowered, the terminal floret rudimentary, club-shaped (tropical Asia) ..... *Centosteca* (including *Ramosia*)

7. Basal floret sterile, represented by lemma only; fertile lemmas bowed out at the base (Africa: Angola, Northern Rhodesia, Kasai and Katanga) ..... *Bromuniola*
7. Basal floret fertile; fertile lemmas not bowed out at the base 8
8. Awns curved, antrorsely scabrous; spikelets 2–3-flowered; nerves of glumes and lemmas weakly developed (Congo) ..... *Chevalierella*
8. Awns straight, rigid, retrorsely scabrous; nerves of glumes and lemmas strongly developed (tropical Asia) ..... *Lophatherum*

Bromuniola Stapf & Hubbard, Bull. Misc. Inform. 1926: 366. 1926.

The type species, *B. gossweileri* Stapf & Hubbard, is the only representative of this West African genus. Stapf and Hubbard, in the original publication (p. 368), state that in general habit the genus resembles *Uniola latifolia* (*Chasmanthium latifolium*) and that it "also recalls some of the Centotheceae, but it differs from these in the presence of a third glume and in the awned valves." Jacques-Félix (1962: 141) reported the distribution as Angola, Northern Rhodesia, Kasai, and Katanga.

Centosteca Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 189. 1810.

A small but widely distributed tropical genus, it is found in southeast Asia, China, Philippines, Japan, Polynesia, northeastern Australia, and tropical Africa. It prefers warm places in semi-shade, has compressed spikelets with 1–3 florets in which the rachilla extends beyond the uppermost floret as a club-shaped rudiment.

The genus *Ramosia* Merrill (Philipp. Jour. Sci. 11: 2. 1916) was based on material collected at the edge of Lake Polog in Sorsogon Province, Philippines. Merrill compared it with *Glyceria* in his discussion of the new genus, but at the same time he expressed dissatisfaction with the alignment. The genus has recently been transferred to *Centosteca* by Monod de Froideville (1971), a disposition with which we concur. In his paper, Monod de Froideville presents a key to the species of the genus.

Chasmanthium Link, Hort. Berol. 1: 159. 1827.

This is a woodland genus of five species, confined mostly to the southeastern and southern regions of the United States except for one species which has also been collected in northern Mexico. For years these species had been placed in *Uniola* and the position of the latter genus remained uncertain until Yates (1966*a*, 1966*b*) reinstated *Chasmanthium* as a genus. The leaves are not clearly tessellate in species of this genus, a feature which departs from the other centostecoid members. Plants of *C. latifolium* occur as far north as Massachusetts, U.S.A., and are thus adapted to cold conditions, unlike most centostecoid grasses which occur in the tropics and subtropics.

Chevalierella A. Camus, Rev. Int. Bot. Appl. Agric. Trop. 13: 421. 1933.

The type species, *C. congoensis* A. Camus, is the only representative of this genus and is known only from the Congo forests. Camus, in her description of the genus, while she did remark that it resembled *Centotheca* and *Lophatherum*, assigned it instead to the tribe Chlorideae and indicated that its affinities were with *Leptocorydion*. Pilger (1954) placed it in the Eragrosteae, Jacques-Félix (1962) in the Centotheceae.

Lophatherum Brongniart *in* Duperrey, Bot. Voy. Coquille 2: 49. 1831.—Type species: *L. gracile* Brongniart.

This is a small genus of forest grasses in tropical Asia with sterile lemmas that project from the top of the spikelet as a tuft of short, stiff awns. Bor (1960) placed the grass with *Centotheca* in the tribe Centotheceae.

Megastachya Palisot de Beauvois, Agrost. 74 (as *Magastachya*), 167 (as *Megastachya*). 1812.—Lectotype: *M. owariensis* P. Beauv., *op. cit.*, Atlas, *pl. 15, fig. 5.* [See Niles & Chase, Contr. U.S. Natl. Herb. 24: 182. 1925.]

This is a monotypic genus from tropical Africa with many-flowered spikelets on long slender pedicels arranged in an open panicle. Chippindall (1955) listed this grass as the sole representative of the Centotheceae in South Africa.

Orthoclada Palisot de Beauvois, Agrost. 69. 1812.—Type species: *O. rariflora* (Lam.) P. Beauv.

A ditypic genus of tropical America and tropical Africa, its members have broad petiolate leaves and compressed spikelets borne in a diffuse panicle. The American species, *O. laxa* (Rich.) P. Beauv., is not rhizomatous like the African one, *O. africana* C. E. Hubbard. In both, the rachilla of the uppermost reduced floret is adnate at its base to the palea of the preceding floret.

Zeugites P. Browne, Civ. Nat. Hist. Jamaica 341. 1756, *nom. cons.*—Type species: *Z. americanus* Willdenow, Sp. Pl. 4: 204. 1805.

This is a genus of about 10 species distributed from Mexico and the West Indies to Andean South America. The plants prefer shaded spots such as ravines, arroyos, and moist pockets on mountainsides, but in spite of their widespread distribution throughout the Americas they seem never to be a common element of the flora. The peculiar spikelet structure of *Zeugites*—with the upper florets male and lowermost one female, becoming gibbous at maturity—is similar to that of *Calderonella* and suggests a close relationship between the two genera. They are easily separated, however, on a number of characters as indicated in the above key to the genera of centostecoid grasses.

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CORRELLIANA (MYRSINACEAE), A NEW PALMOID GENUS OF THE TROPICAL RAIN FOREST[1]

W. G. D'Arcy[2]

Abstract

Correlliana, a new genus, is distinguished from specimens confused with *Clavija* and species confused with *Weigeltia*. The singular growth form, resembling a street lamp on a post, is widespread in tropical rainforests both on continents and islands, and may have evolved in different cases from forest trees or from herbaceous ancestors.

Trees or shrubs which consist of a more or less unbranched, straight trunk and a shock of leaves clustered at the top are referred to in the German literature as *Schopfbaüme* and have been referred to in English as rosette trees or scapose trees, the scape being beneath the rosette instead of above it as in scapose or rosette herbs. The growth form is sometimes simply called palm-like. It is effected not only by true palms but also by many species of dicotyledons. Most palms have compound or digitately dissected leaves as do many palmoid dicots (*Carica*), but in an interesting group of palmoid dicots the leaves are large, narrow, entire or nearly so, and the trees resemble street lamp posts in form. Richards (1966) has noted that this growth form is "fitted only for a permanently favorable environment," and this sort of environment occurs in the tropical rain forest and on some tropical islands. The genus described here evokes some speculation on the palmoid dicots with this street lamp-like growth.

The Genus *Correlliana*

While preparing the treatment of the Theophrastaceae for the *Flora of Panama*, a number of collections came to me tentatively identified as *Clavija*, a mainly palmoid genus of tropical American rain forests. These turned out, upon examination, to belong to the Myrsinaceae, and to a group which hitherto has been confused with *Weigeltia*.

Correlliana D'Arcy, *genus novum*

Type species: *C. spectabilis* (Standl.) D'Arcy.
Weigeltia sect. *Triadophora* Mez *in* Engler, Pflanzenr. 9(IV.236): 291. 1902. Type species: *W. schlimii* (Hook. f.) Mez.

Frutices simplices, foliis grandis, striatis fibris sclerenchymatibus subepidermalibus, floribus 3-merus, fructibus baccatis.

Dioecious, mostly unbranched *shrubs*. *Leaves* large, elliptical to spatulate, entire or serrate margined, coriaceous, pinnately nerved, glabrate, sometimes with minute, scattered gland-like trichomes(?), one or both sides with a well developed subepidermal layer of elongate sclerenchyma fibres running acropetally at an angle slightly flatter than the major veins. *Inflorescence* racemose-

[1] Assisted by the National Science Foundation Grant GB-36202X.
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paniculate, arising terminally, those of the staminate plants slender with short branches, those of the pistillate plants half as long, congested, with longer branches, foliaceous bracts mostly lacking evident subepidermal fibres, the main rachis mostly flattened, sometimes longitudinally grooved, scale-like bractlets present or not. *Flowers* small, 3-merous, the sepals imbricate, drying dark; corolla rotate, deeply lobed, black punctate, the lobes exceeding the calyx; stamens inserted at the top of the corolla tube, filaments short, stout, flattened and narrowing upwards, somewhat longer and more slender in staminate plants, the anthers cordate; ovary napiform, the style short but distinct, the stigmas 3, irregularly expanded, the gynoecium rudimentary in staminate plants. *Fruit* a baccate drupe, globose, apiculate, red; seed 1, hard, globose with a large spheroidal basal excavation; the embryo starchy, circinnate across the basal excavation and compressed against the testa at the top of the seed.

Correlliana is distinct in its 3-parted flowers which are larger than those of *Weigeltia*, in its leaflike bracts, and in the Theophrastaceae-like layer of subepidermal fibres (Fig. 4) on the foliar, but not the floral leaves. These fibres, which appear as striations on the leaf surface, are plainly visible under a hand lens. The wood shows a tendency to break at right angles to the stem and display a radial pattern at the fracture, but this is not so clearly developed as in *Clavija*. The black, glandular spots on the corolla and the curved embryo surmounting the top of the seed cavity place the genus clearly in the Myrsinaceae.

Correlliana takes its name from Donovan S. Correll, a well known and respected American botanist who has made important contributions to both professional and popular aspects of systematic botany.

Hooker (1876) described three species under the genus *Comomyrsine*, one of which is *Correlliana schlimii*. Following Mez's (1902) treatment of the Myrsinaceae, one of the other two species must be chosen to typify *Comomyrsine*, and I select *C. sprucei* Hook. f. as lectotype. Mez considered both *C. sprucei* and *C. simplex* Hook. f., the third species, to be species of *Weigeltia*, and photos of the type specimens of these two species at Missouri (MO) look remarkably like *W. panamensis* (Standl.) Lundell, a true species of *Weigeltia* with 4–5-merous flowers and no sclerenchyma fibres in the leaves. Dr. Peter Goldblatt, Missouri Botanical Garden, kindly examined the type material of these two species of *Comomyrsine* or *Weigeltia* and reported: "I checked the types you asked me about. I am certain that neither has the striations [sclerenchyma fibres] on either leaf surface. The types are by the way the only specimens of either taxon at Kew."

Correlliana apparently embraces several species, and the following transfers are required. The position of *C. chamaephyta* is uncertain. In addition a variety of *C. schlimii*, var. *intermedia*, was described by Moldenke (1947).

Correlliana spectabilis (Standl.) D'Arcy, *comb. nov.*

Ardisia spectabilis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 893. 1938.
Weigeltia triandrae Asplund, Bot. Not. 1939: 802, *t.* 5, *a–d*, 5. 1939.

C. schlimii (Hook. f.) D'Arcy, *comb. nov.*

Comomyrsine schlimii Hook. f., Gen. Pl. 2: 644. 1876.
Weigeltia schlimii (Hook. f.) Mez *in* Engler, Pflanzenr. 9(IV.236): 291. 1902.

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C. multiflora (A. C. Smith) D'Arcy, *comb. nov.*

Weigeltia multiflora A. C. Smith, Bull. Torrey Bot. Club 60: 387. 1933.

C. chamaephyta (Diels) D'Arcy, *comb. nov.*

Weigeltia chamaephyta Diels, Notizblatt 15: 383. 1941.

No types of *Correlliana* were seen and no material was seen of the two last mentioned species, so no key is provided at this time. Only one sheet of *Correlliana schlimii* (*Lawrence 530*, Colombia) has been seen. In *C. schlimii* the inflorescence branches are much longer and the bractlets much smaller than in specimens from Central America identifiable as *C. spectabilis*.

In his recent treatment of the Myrsinaceae for the *Flora of Panama*, Lundell (1971) included two species under *Weigeltia*, *W. spectabilis*, which was illustrated and which is a species of *Correlliana*, and *W. panamensis* Standl. Lundell cited one specimen under each species, that of *W. panamensis* being the type of the species. Since Lundell's paper, several new collections of *Correlliana spectabilis* from Central America have come to light, mostly from pidgeon-holes labelled "*Clavija*-indets." The species is apparently common on Cerro Campana, a lowland peak some 50 km west of Panama City on the Pacific side of the isthmus. One such collection, *Croat 14700* (MO, Fig. 1), superficially matches *Weigeltia panamensis* in its short congested inflorescences, and it also superficially matches type photos of *W. simplex* and *W. sprucei*. Recourse to a hand lens discloses that it is quite distinct from these, and its singular appearance is due to its being pistillate, and the only such collection seen. In this species the two sexes display greater difference in the gross appearance of the inflorescence than in any other part of the plant except the gyneocium (see Figs. 1–3).

The Convergence of *Clavija* and *Correlliana*

The palmoid growth form, the hard, globose seeds, the racemose inflorescences, the sclerenchyma fibres beneath the leaf epidermis, and the dioecious sexual condition are much alike in *Correlliana* and most species of *Clavija*. Some writers (Solereder, 1899; Hooker, 1876; Pax, 1899) have considered the Theophrastaceae as a tribe of the Myrsinaceae, but more recently it has been considered a separate family. Appendages on the corolla, usually referred to as staminodes, distinguish the flowers of the Theophrastaceae, and histological details (from Metcalfe & Chalk, 1950) such as a dissected vascular system, absence of septate fibres, and secretory elements further support recognition of the family. Although glandular dots are present on the foliage, these are not like the black-punctate dots on most Myrsinaceae. Most Myrsinaceae, at least those in the tribe Myrsineae which includes *Weigeltia*, have curved embryos quite

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Figures 1–4. *Correlliana spectabilis* (Standl.) D'Arcy from Panama.—1. Pistillate plant in flower. [After *Croat 14700* (MO).]—2. Pistillate plant in fruit. [After *Smith & Smith 3346* (F).]—3. Staminate plant in flower. [After *Luteyn 1021* (DUKE).]—4. Leaf underside of *Croat 14700* (MO) showing subepidermal sclerenchyma fibres which run across the veins. [×12.]

TABLE 1. Species which commonly assume the street lamp form of palmoid growth habit. Some branch sparingly when they eventually reach the forest canopy. All are from rain forests and most from the tropics.

SPECIES	FAMILY	PLACE OF OCCURRENCE
Adeniscanthus fusciflorus Ducke	Rutaceae	Amazonian Peru
Asplenium nidus L.	Polypodiaceae	Java
Anthocleista nobilis G. Don	Loganiaceae	Tropical West Africa
Cespedezia macrophylla Seem.	Ochnaceae	Tropical America
Clavija spp. (Most of genus)	Theophrastaceae	Tropical America
Cyanea leptostegia A. Gray	Lobeliaceae	Hawaiian Islands
Delissea undulata Gaud.	Lobeliaceae	Hawaiian Islands
Dendroseris macrophylla D. Don	Compositae	Juan Fernandez
Dracaena sp.	Liliaceae	Old World tropics
Euphorbia valerii Standl.	Euphoribiaceae	Central America
Ficus pseudopalma Blanco	Moraceae	Philippines
Gustavia sp.	Lecythidaceae	Tropical America
Pausandra trianae Baill.	Euphorbiaceae	Tropical America
Pentagonia macrophylla Benth.	Rubiaceae	Panama
Phyllobotryon soyauxianum Baill.	Flacourtiaceae	Tropical West Africa
Plantago princeps Cham. & Schlecht.	Plantaginaceae	Hawaiian Islands
Potalia amara Aubl.	Loganiaceae	Tropical America
Sarcocephalus vanderguchtii de Willd	Rubiaceae	Tropical West Africa
Weigeltia sprucei (Hook. f.) Mez	Myrsinaceae	Tropical America

unlike those in the Theophrastaceae. Although these differences probably warrant recognition of two families, most writers consider them to be closely related. If the two families are closely related, it is not through a *Clavija-Correlliana* link. Apart from the manifest differences in flower and embryo which make such a junction seem unlikely, a link at this point between the two families would presume that at least one of the genera is primitive in its family. Features of *Clavija* strongly suggestive of advancement within the Theophrastaceae are the imperfect flowers, few ovules in many species, and the connate androecium. There is little about *Correlliana* to suggest it is primitive within the Myrsinaceae, while 3-merous flowers, dioecious plants, and subepidermal sclerenchyma fibres may all be considered specializations. *Clavija* is the most specialized genus in the Theophrastaceae, and *Correlliana* is not primitive in the Myrsinaceae. It is safe to say that these two genera represent converging end points in the evolution of two related families, and consequently, the street lamp sort of palmoid growth habit should be considered a specialization in these two cases. "Groups which have undergone parallel evolutionary change may well have been rather similar to begin with" (Cronquist, 1968), but before applying this reasoning to the case at hand, it is instructive to examine some other cases of similar growth form.

THE PALMOID GROWTH FORM

A few examples of species with the street lamp sort of palmoid growth are listed in Table 1. These examples have features in common. The leaves are large (more than 30 cm, often 70 cm or more long), somewhat coriaceous, oblanceolate or narrowly elliptic, entire or toothed but the teeth mostly low in profile; the leaf base is narrowed in the lower portion to an abrupt or indistinct junction

with a stout or indistinct petiole; the trunk is slender, mostly unbranched and may be few to many meters tall; and the crown may take the form of a dense ball of leaves. It is not unusual for juveniles and adults to have leaves of somewhat different shape, and in some species a drip tip is present.

From a systematic point of view some genera, *e. g. Clavija, Correlliana*, are made up of predominantly street lamp-like forms, but other cases are isolated instances in a diverse list of families. Some of the examples are from families commonly considered woody, while others, *e. g. Plantago, Cyanea*, are from families commonly considered herbaceous. The list includes ferns and monocots, where the stem structure is not homologous with the secondarily produced stems of the dicots. In distribution, some are found on continental mainlands and others on islands, but all are found in wet forests, and all are found in tropical rain forests except *Dendroseris* from cloud forests on temperate Juan Fernandez.

Richards (1966) noted that "a number of large rain-forest trees, which later have normally branched crowns, remain unbranched with their leaves crowded on to the last few centimeters of the stem until they are 6–7 m or more high, *e. g.* the South American *Sterculia puriens* and *S. rugosa*." A few pages further in the same work, he illustrated leaves of *Lophira procera* (Ochnaceae–West Africa) in which the sapling leaves appear like those of the palmoids cited here and the adult leaves are smaller and different in shape. Richards went on to say that while no satisfactory explanations have been advanced for the particular stresses under which these forms confer selective advantage, "the extraordinary similarity of the foliage among rain-forest trees of the most varied systematic affinities cannot be due to chance."

Although the palmoid growth and the unbranched, essentially entire leaved form considered here must be nearly as old as the tropical rain forest itself, the heterogeneous origin of the examples provided does not argue for any great antiquity for the bulk of the cases considered. If the flora of the tropical rain forest has been continuous from the early evolution of the angiosperms, we might expect many taxa numerous in species with this form throughout the older rain forest. A likely explanation is that the palmoid street lamp, or *Schopfbaum* form, is of short duration and is redeveloped from different taxa at different times.

In Carlquist's (1965) words, "a tree seedling in a forest encounters a difficulty: growing up into better-lit upper reaches of a forest, very shady conditions must at first be encountered," and he postulated: "*Sarcopygme*'s trunk branches only a few times—or not at all—certainly the most efficient way to reach the upperportions of a forest." Such a plant may have an advantage if it can bloom and fruit before reaching the canopy, and some of the palmoid species may be the product of such a nanophytism, precocious bloomers which never attain a "mature" structure. When the plant does reach the canopy, the unbranched form is of little apparent advantage, and in many forest species, branching begins as the plant approaches or reaches the canopy. In the absence of features selecting against branching in the canopy, species of more usual branching and leafing habit, which under the influences of the rain forest evolve toward branchlessness and large, oblanceolate leaves, are likely to retain their capacity for branching at maturity indefinitely, even if few individuals ever reach the canopy.

Even in cases where a species has apparently lost its capability for reaching the canopy and branching in it, it is not unreasonable to suppose that a change in conditions might lead to a "re-evolution" of branching growth. Oppenheimer and Lang (1969) have recorded that monkeys may stimulate branching in *Gustavia superba*.

Carlquist has made much of the belief that insular environments encourage the evolution of woody plants from herbaceous ancestors. Citing many examples, among which the Compositae, Lobeliaceae and Cruciferae are favored, he has argued for a situation where a herbaceous species from a temperate or seasonal environment when placed in an environment perpetually favorable for growth continues to grow without senescence until the stature of a tree is attained. He also supports Darwin's (1859) suggestion that in a community of herbs, a species "might readily gain an advantage by growing taller and taller and overtopping the other plants." There is some substance in both of these proposals, but neither is particular to islands. The Darwinian suggestion is more true of forests than herbaceous communities, and no other reason is so convincing to explain the height of tall forests anywhere in the world. The perpetual summer hypothesis elaborated by Carlquist is applicable to tropical, moist forests on continents as well as to insular environments. An important assumed difference is that islands are more open to introduction of new elements—have more unfilled niches—than continental communities and hence are more likely to host successful herbaceous introductions from non-equable regions. Of Carlquist's examples of trees with herbaceous or shrubby ancestry in insular sites, a number are trees and these are shaped like street lamps and are restricted to the tropical rain forest habitats on the islands. In Table 1, *Dendroseris*, *Cyanea*, and *Plantago* can be traced to groups familiar in other parts of the world as herbs; and *Euphorbia*, *Pausandra*, and *Sarcopygme* are traceable to forms very different from that of the species noted. It is likely therefore, that the palmoid street lamp growth form has arisen in at least two ways; as a form which appears when some herbaceous groups evolve into woody growth, and as a nanophytic form of forest trees which have found it unnecessary to reach the forest canopy.

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MATERIALS FOR A TREATMENT OF *COLUMNEA* IN PANAMA[1]

BRIAN MORLEY[2]

A number of taxonomic changes and observations have resulted from a study of Panamanian *Columneas* and these are discussed below.

1. Recognition of taxonomic sections within *Columnea* sens. lat.—Experimental work on cultivated *Columneas* and herbarium work have led me to regard leaf anisophylly as an unreliable taxonomic character for all but a few large-leaved species, and for this reason I do not recognize the differences between sections *Collandra* and *Stygnanthe* or *Columnea* and *Cryptocolumnea*.

The differences between sections *Stenanthus* and *Ortholoma*, based on sepal shape and adaxial leaf vestiture, are also unreliable and arbitrary in my opinion and are not followed here. There is much work needed on the floral morphology of *Columneas*, but I think that present knowledge will allow the construction of a sectional classification based on corolla morphology, despite the views of those suggesting that such a classification is simply a classification of the pollen vectors associated with different corolla shapes. Breeding relationships suggest that corolla morphology is more than simply an indicator of the type of pollinator which visits the flowers (Morley, in press). On the basis of corolla morphology I have transferred some species usually placed in sections *Collandra* and *Stygnanthe* into sect. *Pterygoloma*, which hitherto contained only one species. Figure 1 shows representative corollas from the sections recognized in Panama and listed below with synonymy.

Columnea L. sect. *Collandra* (Lem.) Benth. & Hook. (1876).

Syn. sect. *Stygnanthe* (Hanst.) Benth. & Hook. (1876).

Columnea L. sect. *Ortholoma* Benth. (1846).

Syn. sect. *Stenanthus* (Oerst. *ex.* Hanst.) Fritsch (1893).

Columnea L. sect. *Pterygoloma* (Hanst.) Fritsch (1893).

Syn. sect. *Trichantha* (Hook.) Kuntze (1904).
sect. *Collandra* sensu Morton (1971), pro parte.
sect. *Stygnanthe* sensu Morton (1971) pro parte.

Columnea L. sect. *Pentadenia* (Plach.) Benth. & Hook. (1876).

Columnea L. sect. *Columnea*

Syn. sect. *Cryptocolumnea* (Hanst.) Benth. & Hook. (1876).

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[1] I wish to thank the late C. V. Morton for help with nomenclatural problems and Professor John O'Meara and R. D. Meikle for correcting the Latin diagnoses.

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ANN. MISSOURI BOT. GARD. 60: 449–460. 1973.

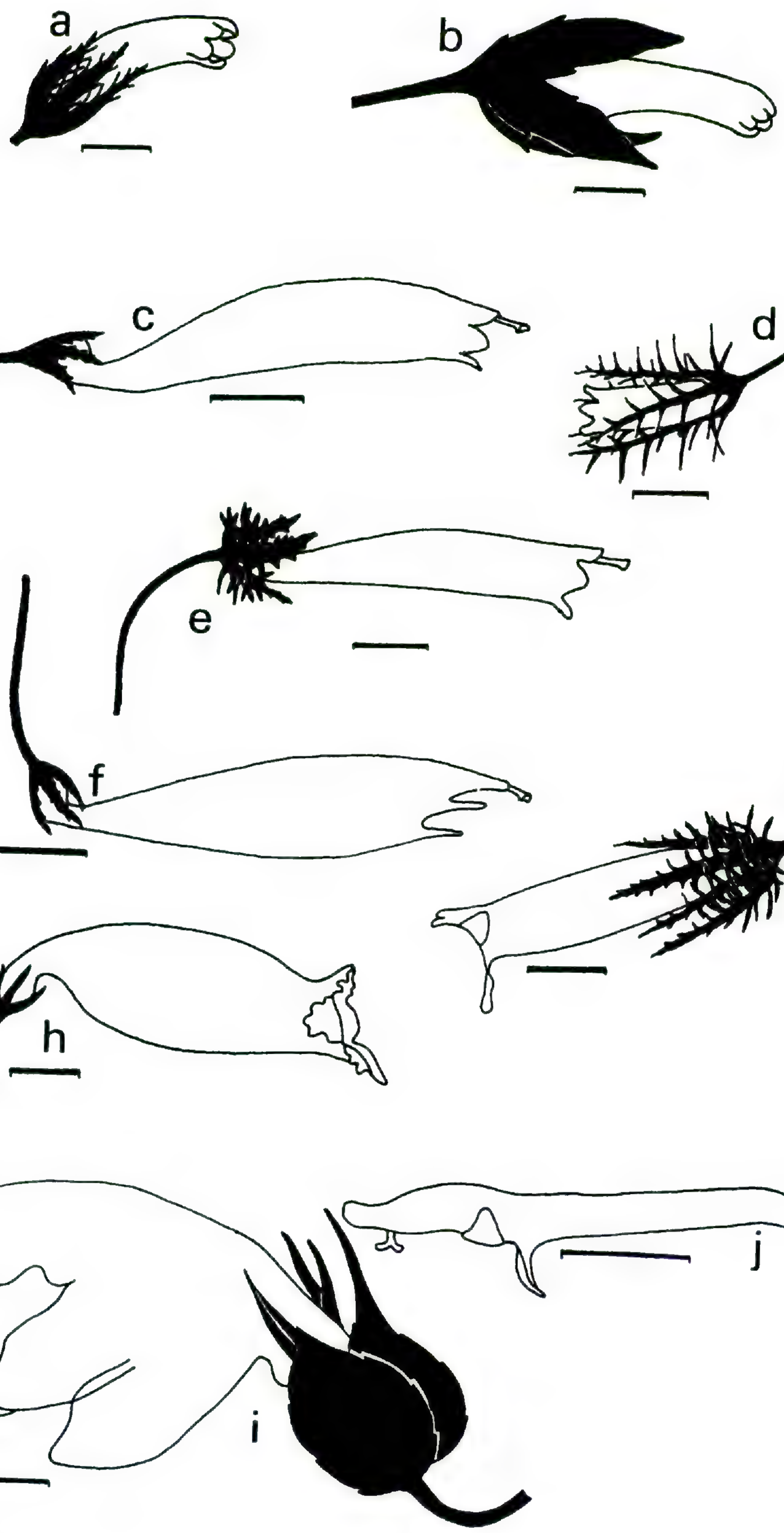

FIGURE 1. Corolla morphology in sections of *Columnea*.—Sect. *Collandra*: a, *C. aureonitens* Hook. (Colombia); b, *C. dissimilis* Morton (Panama); d, *C. segregata* Morley (Panama).—Sect. *Pterygoloma*: e, *C. silvarum* Morton var. *butcheri* Morley (Panama); e, *C. moorei* Morton (Panama).—Sect. *Ortholoma*: f, *C. mira* Morley (Panama); g, *C. sanguino-*

Section **Collandra**

2. *Columnea consanguinea* Hanst. from Panama has adpressed abaxial leaf vestiture unlike the more erect abaxial vestiture of Costa Rican plants. As *C. consanguinea* was originally described from Costa Rica, and all Panama material has adpressed vestiture, it is proposed to recognize a new variety in Panama.

Columnea consanguinea Hanst. var. **adpressa** var. nov.

A var. *consanguinea* differt foliis subtus pilis adpressis.

Differing from var. *consanguinea* by the adpressed hairs on the leaf undersides.

Holotype: PANAMA. PROV. CHIRIQUI: Western slopes of Cerro de la Horqueta, Bajo Mono-Robalo Trail, altitude 5000–7000 feet, *Allen 4788*, July 27, 1947 (US). Isotype: (MO). Topotype: *Allen 4924* (US, MO).

3. There are few morphological discontinuities between *Columnea darienensis* Morton and *C. consanguinea* var. *adpressa*. The flower of the type of *C. darienensis* (*Pittier 5660*, US) is damaged with one of the corolla lobes appearing to spread, but the other two undamaged lobes have a typical incurved appearance of many species in sect. *Collandra*. *Pittier 5660* has corolla vestiture and dimensions close to those of *C. consanguinea*, and as *C. darienensis* have poorly serrate sepals (*Duke & Elias EI3694*, MO) and some *C. consanguinea* do not have entire sepals (*Allen 4788, 4924*, US), this distinction breaks down. Some *C. darienensis* (*Terry 1547*, GH) are reported with the same yellow corollas which are supposed to characterize *C. consanguinea*, instead of orange-scarlet. *Columnea darienensis* has not yet been found with red abaxial leaf coloring which is common in *C. consanguinea*, and furthermore the leaf vestiture of *C. darienensis* is more sparsely strigose, corollas less sericeous, and sepals tend to be more often serrate. In order to relate the variation of *C. darienensis* more closely with *C. consanguinea* I propose to make *C. darienensis* a variety of *C. consanguinea*.

Columnea consanguinea Hanst. var. **darienensis** (Morton) Morley, comb. nov.

Basionym: *C. darienensis* Morton, Ann. Missouri Bot. Gard. 29: 46. 1942.

4. *Columnea dissimilis* Morton was described in 1942 from El Valle de Anton, Prov. Coclé (*Allen 2483*, US) and is thought to be endemic to the area. Comparison between *C. dissimilis* and *C. translucens* Raymond, known only in cultivation and from an unknown source, shows the latter to be almost identical with *C. dissimilis*.

C. translucens (*Soulier s. n.*, US) has reddish sepals which breaks down the distinction with *C. dissimilis* based on sepal colour. Likewise the appearance

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←

lenta (Klotzsch *ex* Oersted) Hanstein (Panama); h, *C. warscewicziana* (Klotzsch *ex* Oersted) Hanstein (Panama).—Sect. *Pentadenia*: i, *C. incarnata* Morton (Panama).—Sect. *Columnea*: j, *C. tomentulosa* Morton var. *tulae* (Urban) Morley (Greater Antilles). [The scale by each corolla represents 1 cm in length.]

of orange corollas in *C. translucens* can be explained by less dense red hairs superimposed upon yellow corolla tissues; in *C. dissimilis* the yellow corolla tissue does not show through a thick covering of red hairs on the tube. The only notable difference which *C. translucens* exhibits is the possession of glandular hairs in all parts, although the type of *C. dissimilis* (*Allen 2483*) is not devoid of them. Possession of glandular hairs is thought insufficient reason to maintain *C. translucens* at specific level, and lack of provenance of *C. translucens* material leads me to reduce the taxon to synonymy with *C. dissimilis* pending further information on the distribution of *C. translucens*.

Columnea dissimilis Morton, Ann. Missouri Bot. Gard. 29: 47. 1942.

Syn. *C. translucens* Raymond, Bot. Not. 114: 351. 1961.

Section **Columnea**.

5. *Columnea conferta* Morton was described in synonymy with *C. citrina* Morton if the isotype (*Terry & Terry 1554*, GH) of *C. conferta* is identical to the holotype (F, not seen). A fundamental similarity between the type descriptions led to closer examination of the corolla morphology of *C. conferta*, and was found to place the taxon in sect. *Columnea* and not *Collandra*. The isotype of *C. conferta* has a bilabiate corolla in the bud burst condition. Detailed examination of calyx lobe shape and margin, abaxial leaf vestiture and pigmentation and corolla pigmentation of the types of both taxa confirm that *C. conferta* is a synonym of *C. citrina*. It is therefore not surprising that *C. conferta* is known only from the type collection but *C. citrina* has been collected on several occasions.

It may be that *C. conferta* was mistakenly described as belonging to sect. *Collandra* by the use of immature flowering material as the young buds of *C. citrina* (*Allen 2404*, US) bear some resemblance to fully opened flowers of species in sect. *Collandra*. To support this view the type description of *C. conferta* states the corolla is "verisimiliter paullo bilabiato" indicating some doubt in the interpretation of corolla shape.

Columnea citrina Morton, Ann. Missouri Bot. Gard. 29: 44. 1942.

Syn. *C. conferta* Morton, Ann. Missouri Bot. Gard. 29: 44. 1942.

6. *Columnea nicaraguensis* Oersted was found to exhibit much variation in leaf shape, but sepal shape and sepal, leaf and corolla vestiture made it possible to identify specimens without difficulty. Figure 2 shows the scatter diagram for a plot of leaf length against leaf width at the widest part for large leaves of the Panamanian specimens seen.

7. *Columnea microcalyx* Hanst. was described in 1865 from Costa Rica, and in 1901 Donnell Smith described the variety *macrophylla* also from Costa Rica. In 1938, Morton, wishing to raise var. *macrophylla* to specific rank found it necessary to use a new epithet "localis," *C. localis* Morton, because of the existence of *C. macrophylla* Kuntze (1891). Study of the variation of *C. microcalyx* and *C. localis* has led me to regard the latter as a variety of the former, so that Donnell Smith's var. *macrophylla* should be reinstated.

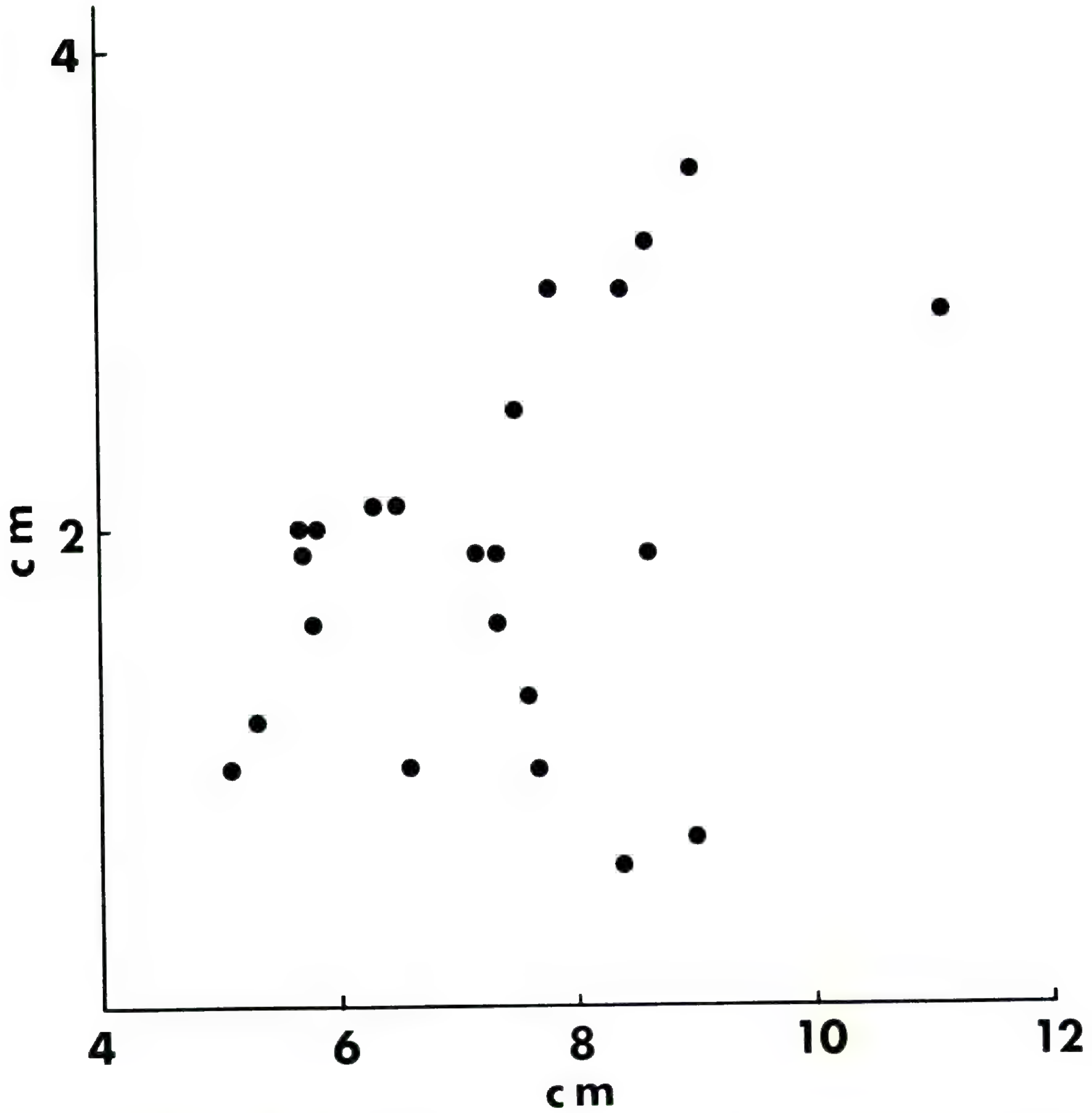

FIGURE 2. Scatter diagram of leaf length (horizontal axis) against leaf width for larger leaves of Panamanian *Columnea nicaraguensis*.

The example of variation in *C. localis* and *C. microcalyx* shown in Table 1 concerns three collections. *Allen 1428* (GH, US, MO) are all identified as *C. localis* by Morton; *Davidson 76* (MO) is misidentified as *C. tomentosa*, while *Skutch 3215* (MO) is identified as *C. microcalyx* by Morton. It can be seen that the three specimens collected by Allen, presumably from the same site, each show a different combination of *C. localis* and *C. microcalyx* characters.

Columnea microcalyx and *C. localis* can only be consistently distinguished by the use of leaf and stem vestiture and leaf length. Differences based on sepal shape and pedicel length intergrade; for example *Allen 4381* (US), identified by Morton as *C. localis*, agrees with the description of that taxon, but the same collection (MO) has sepals with a blunt tip and short pedicels, both characters characterizing *C. microcalyx*. Likewise, *Pittier 5625* (US) is like *C. localis* apart

TABLE 1. Variation in characters of *Columnea localis* and *C. microcalyx*.

Collection	Character							
	Stem hairs		Leaf vestiture		Pedicel length		Sepal tip	
	Adpressed (*mic.*)	Spreading (*loc.*)	Strigose (*mic.*)	Spreading (*loc.*)	Short (*mic.*)	Long (*loc.*)	Obtuse (*mic.*)	Acute (*loc.*)
Allen 1428, GH	×		×			×	×	
Allen 1428, US		×	×			×		×
Allen 1428, MO	×		×			×		×
Davidson 76, MO		×	×			×		×
Skutch 2315, MO	×		×		×		×	

from having short pedicels. Woodson *et al. 955* (MO) has somewhat sparsely hairy leaves for *C. localis* but is otherwise satisfactory. Both var. *microcalyx* and var. *macrophylla* occur in Panama.

Columnea microcalyx Hanst. var. *microcalyx*, Linnaea 34: 408. 1865.

C. microcalyx var. *macrophylla* Donn. Sm., Bot. Gaz. (Crawfordsville) 31: 118. 1901.

Syn. *C. localis* Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1165. 1938.

8. *Columnea billbergiana* Beurl. was described in 1854, being based on material collected by Billberg from Porto Bello, Prov. Colón, Panama. The species is found only in Panama and is held to differ from *C. percrassa* Morton by having red sepals (but the type of *C. percrassa* (US) and a topotype have sepals with traces of red pigment), by having scarlet corollas (but as with *C. percrassa* there is sometimes a small yellow area at the throat of the corolla), and by having brown instead of olive stems as in *C. percrassa* (but some old *C. percrassa* plants with dappled axes suggest that these also turn brown, *i. e.* become non-photosynthetic).

All known *Columnea percrassa* herbarium material comes from the type locality of Cerro Campana, Prov. Panamá, altitude 400 m, and all cultivated material from an unknown locality, so there was reason to examine the validity of *C. percrassa* as a species. *Columnea billbergiana* also grows on Cerro Campana and comparison of *C. percrassa* with this material has shown the two are the same. The type of *C. percrassa* (*Allen 2432*, US) has sepals only slightly less hairy than those of *C. billbergiana* (*Allen 2428*, US, MO), which have densely hairy sepals and pedicels. Sepal margins in *C. percrassa* type show as much basal toothing as certain *C. billbergiana* specimens (*Allen 1651*, US). The shape of the leaves of type *C. percrassa* is indistinguishable from certain *C. billbergiana* specimens (*Allen 2428*; *Porter 4273*, and *4948*, all MO), instead of being less acute than in *C. billbergiana*. *Columnea percrassa* as identified by Morton (*Hutchison & Dressler 2952*, MO) has traces of red pigment on the undersides of the leaves yet the pigment is held to occur only in *C. billbergiana*. These observations lead me to reduce *C. percrassa* to synonymy with *C. billbergiana*.

Columnea billbergiana Beurl., Svensk. Vet. Handl. 1854: 135. 1854.

Syn. *C. percrassa* Morton, Baileya 7: 59. 1959.

9. *Columnea tenuis* Kl. *ex* Oerst. was described from material collected in Prov. Veraguas, Panama, by Julius von Warscewicz. *Columnea obliqua* Morton is held to differ from *C. tenuis* in having entire sepals (but type *C. obliqua* has slightly toothed sepals like some *C. tenuis*), in having green sepals (but sepals are reddish in type *C. obliqua*), in having leaves which are oblique at the base (also seen in some *C. tenuis*), and in having different leaf and corolla dimensions (dimensions which are found to overlap). The corolla color of the two taxa is the same in some specimens, and both sometimes show red abaxial leaf surfaces. These observations lead me to reduce *C. obliqua* to synonymy with *C. tenuis*. The difference of leaf shape between *C. tenuis* and the closely related *C. oerstediana* Kl. *ex* Oerst. was seen to be constant.

Columnea tenuis Kl. *ex* Oerst., Centralamer. Gesner. 63. 1858.

Syn. *C. obliqua* Morton, Ann. Missouri Bot. Gard. 29: 49. 1942.

10. *Columnea hirta* Kl. & Hanst. was described from material collected in Prov. Veraguas, Panama, by Warscewicz, but the type has probably been destroyed in Berlin. I have seen no Panamanian collection of this species, but the closely similar *C. mortonii* Raymond is Panamanian. *Columnea hirta* and *C. mortonii* are said to differ in the color of the stem hairs, leaf shape, bract shape, calyx lobe toothing, and hairiness of the filaments. However, *C. mortonii* identified by Raymond (*Soulier s. n.*, US) has oblong leaves, reddish stem hairs, lacks red-based calyx hairs (all of which are *C. hirta* characters), and has no sepal teeth unlike both *C. hirta* and *C. mortonii*. This material was apparently from the same source as the type material, from the Fairchild Tropical Garden, Miami, Florida. *Peele 111* (US), from Longwood Gardens, also has traces of red stem hairs and lacks red-based calyx hairs, yet Longwood plants are stated to represent *C. mortonii* by Morton (1971). I have not seen specimens of *Dressler 3469* and *3848* from Cerro Jefe, Prov. Panamá, which Wiehler (1970) refers to *C. mortonii*.

Until further material of *C. hirta* is collected from Panama I propose to make *C. mortonii* a Panamanian variety of *C. hirta*, which is known to occur in Costa Rica. Subsequent collections may require that *C. mortonii* be made synonymous with *C. hirta*.

Columnea hirta Kl. & Hanst. var. *hirta* Linnaea 34: 403. 1865.

Syn. *C. hirsuta* Kl. *ex* Oerst., Centralamer. Gesner. 61. 1858, *non* Swartz.

C. hirta Kl. & Hanst. var. *mortonii* (Raymond) Morley, comb. nov.

Basionym: *G. mortonii* Raymond, Bot. Not. 114: 346. 1961.

11. *Columnea tomentulosa* Morton was described in 1938 to replace the later homonym of *C. tomentosa* Roxb. (1814), *C. tomentosa* Oerst. (1858). Comparison of *C. tomentulosa* with *C. tulae* Urb. from Puerto Rico and Hispaniola shows that apart from possessing more highly toothed sepals and being smaller

TABLE 2. Comparison of pedicel length and sepal tooth length in *Columnea grata* and *C. sanguinolenta*.

Specimen	Pedicel length (cm)	Speal tooth length (mm)
Columnea grata		
Oersted 9288 i	11.1	2
Oersted 9288 ii	10.0	2
C. sanguinolenta		
Siebert 1562	4.5	10
Wedel 942	3.0	7
Wedel 1513	3.4	8
Wedel 2325	2.7	4
Kirkbride et al. 567	3.4	8
Standley et al. 45757	3.9	12
Dunlap 449	2.5	5

in all parts, *C. tomentulosa* is very close to *C. tulae*. It is proposed to relate Central American *tomentulosa* to the variation pattern of *C. tulae* by making the latter a variety of the former. (There is a parallel variation pattern found in *C. scandens* L. where certain Lesser Antillean populations of var. *scandens* have variously toothed sepals and differ in leaf size from mainland populations of var. *fendleri* (Sprague) Morley from Venezuela.) Conspecificity of *C. tulae* with *C. tomentulosa* supports the independently arrived at conclusion that *C. tulae* probably arose from Central American ancestors rather than South American as is the case in *C. scandens* (Morley, 1972). The distribution of var. *tomentulosa* along the Atlantic side of Central America supports relationship with the Greater Antillean var. *tulae*.

Columnea tomentulosa Morton var. *tomentulosa* Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1169. 1938.

Syn. *C. tomentosa* Oerst., Centralamer. Gesner. 64. 1858.

Columnea tomentulosa Morton var. *tulae* (Urban) Morley, comb. nov.

Basionym: *C. tulae* Urban, Symb. Antill. 1: 409. 1899.
Syn. *C. tulae* Urban var. *rubra* Urban, Symb. Antill. 1: 409. 1899.
C. tulae var. *flava* Urban, Symb Antill. 1: 409. 1899.

12. A loan of Oersted material from Copenhagen included some Panamanian specimens, the details of the sheets being as follows.

Columnea sp. (as *Stenanthus serratus*), one sheet, single shoot, no corolla, no fruit; "No. 188, *Columnea serrata, Stenosacanthus serratus, Stenanthus* Oersted, Cult.?"—This specimen was clearly not *C. serrata* (Kl.) Hanst., the type of which is probably destroyed in Berlin.

Columnea tomentulosa Mort. var. *tomentulosa* (as *Columnea tomentosa*), one sheet, single shoot, no corolla, no fruit; "*Oersted* 9293, Nicaragua: River (?) S. Juan, det. Kränzlein."—ISOTYPE.

Columnea magnifica Kl. & Hanst. *ex* Oerst. (as *C. magnifica*), one sheet, one shoot tip, leaves and two damaged corollas in packet; "*Columnea magnifica* Kl. Costa Rica, Warscewicz, Spec. Orig. 22700."

Although *Columnea grata* Morton is not recorded from Panama, it is similar to *C. sanguinolenta* (Kl.) Hanst. which does, so that the two can be compared. *Columnea grata* Morton (as *Stenanthus heterophyllus*), 3 sheets, all organs present except fruit; "Oersted Pl. Centram. 9288, *Columnea heterophylla*, *Stenanthus heterophyllus* Oerst., prope Naranjo 5/49."—HOLOTYPE. Table 2 compares pedicel length and sepal tooth length in *C. grata* and *C. sanguinolenta*, showing the two are distinct.

New Taxa.

13. **Columnea silvarum** Morton var. **butcheri** var. nov. (Sect. *Pterygoloma*)

Differt a var. *silvarum* sepalis brevioribus et sepalis et pedicellis pilis fuscis vestita.

Differing from var. *silvarum* by the shorter sepals and sepal and pedicel hairs dull brown.

Woody *herb*; stems about 7 mm in diameter, purplish-dull brown tomentose. *Leaves* of a pair unequal, the larger oblanceolate, acuminate, oblique at base, serrate, about 10.3 cm long and 2.3 cm wide at widest point, adaxially hirsute-tomentose with 2–3-celled white adpressed hairs and 7–10-celled reddish erect fine hairs, abaxially hirsute-tomentose with 5–8-celled reddish erect fine hairs, blades green above and beneath but with reddish cast produced by indumentum, petioles about 2 mm long, the smaller leaves about 2.1 cm long and 5 mm wide, lanceolate, acuminate, serrate, green above and beneath, vestiture as in larger leaves. *Flowers* in clusters of 3 or more, bracteate, bracts about 5 mm long, linear, dull brown tomentose, pedicels to about 2 cm long, dull brown long tomentose; sepals lanceolate, acuminate, 3–4 toothed, teeth linear, to 1 mm long, sepals green, about 8 mm long and 1 mm wide at middle, externally dull brown tomentose; corollas tubular, slightly zygomorphic, yellow with lobes having reddish crescent marks, about 3.7 cm long, about 3 mm in diameter at base, becoming about 7 mm in diameter in middle then 5 mm in diameter at throat, lobes slightly unequal, lobed portion about 4 mm long, spreading, corolla externally pilose, hairs transparent, filaments glabrous, yellow, anthers included, 1 mm long and 1.5 mm wide, style glabrous, yellow, stigma stomatomorphic, ovary white pilose, disk gland bilobed, fruit not seen.

Holotype: PANAMA. PROV. CHIRIQUÍ: Near village Cuesta de Piedra, near Río Escarria, altitude 3600 feet, *Butcher s. n.*, March 1962 (US).

This variety is known also from Costa Rica (Pittier *11196*, US). It is close to *C. silvarum* in its characters.

14. **Columnea mira** sp. nov. (Sect. *Ortholoma*)

A *Columnea ochroleuca* (Kl. *ex.* Oerst.) Hanst. differt corollis flavis et rubris, foliis oblanceolatis et caulibus rutilis et hispidis.

Differing from *Columnea ochroleuca* (Kl. *ex* Oerst.) Hanst. by the yellow and red corollas, oblanceolate leaves and reddish purple hispid stems.

Woody *herb*; epiphytic, stems 3–4 mm in diameter, red-purple hispid when young. *Leaves* of a pair unequal, the larger oblanceolate: acute, oblique at base, crenate-serrate, about 5.3–8.1 cm long and 2.1–2.8 cm wide at widest point, adaxially densely hirsute with 2–3-celled white adpressed hairs and 4–8-celled reddish or red erect hairs, abaxially densely hirsute with 2–3-celled white adpressed hairs and 5–9-celled red erect hairs, blades green above but conspicuously red hirsute, blades concolorous red-purple beneath, petioles absent or to 2 mm long, the smaller leaves lanceolate, acuminate, serrate, about 8 mm long and 3 mm wide, green above, red purple beneath, indumentum as larger leaves. *Flowers* solitary or paired, bracteate, bracts about 4 mm long, linear, brown reddish pilose, pedicels 1.1–1.6 cm long, dull brown-red pilose; sepals lanceolate, acuminate, 2–3 toothed, teeth linear, to 2 mm long, sepals green, about 8–10 mm long and 1.5 mm wide in middle, externally red-purple-brown hirsute; corollas tubular, zygomorphic, yellow with two long brownish red stripes running from sinuses of anterior lobe and two shorter paler red stripes running from sinuses between lateral and posterior lobes, about 4.6 cm long, about 3 mm in diameter at base becoming about 11 mm in diameter in middle then 8 mm in diameter at throat, lobes unequal, posterior lobes about 7 mm long, bilobed at apex, lobed portion of corolla about 9 mm long, anterior lobe about 6 mm long, all lobes spreading and narrow, corolla externally reddish pilose, filaments glabrous, yellow, anthers exserted, 1 mm long and 1.2 mm wide, style glabrous, reddish, stigma stomatomorphic, ovary reddish pilose, disk gland bilobed, fruits not seen.

Holotype: PANAMA. PROV. PANAMÁ: Cerro Jefe summit, altitude 2900 feet, *Dwyer et al.* 7236, March 12, 1967 (MO). Topotypes: Dwyer *et al.* 5038 (DBN), *Butcher 1* (US).

This species will make a most ornamental addition to cultivated *Columneas*. The type of *C. ochroleuca* I have not seen, as it was destroyed in Berlin together with other types of Warscewicz collected in Prov. Veraguas, Panama. Without type material of *C. ochroleuca* it is difficult to know whether *C. mira* should be given specific rank. In the absence of other data I have given *C. mira* specific rank.

15. **Columnea cruenta** sp. nov. (Sect. *Pterygoloma*)

A *Columnea perpulchra* Morton differt sepalis brevioribus, foliis angustioribus, caulibus indumento pilorum rutiliorum densius vestitis.

Differing from *Columnea perpulchra* Morton by the shorter sepals, narrower leaves, red stem hairs, and denser indumentum.

Woody *herbs*; epiphytic, stems about 5 mm in diameter, brown-purple hirsute. *Leaves* of a pair unequal, the larger oblanceolate, acuminate, oblique at base, serrate, about 13 cm long and 3.5 cm wide at widest point, adaxially pilose with 4–5-celled reddish erect hairs, abaxially pilose with 2–3-celled white adpressed hairs and 5–6-celled reddish erect hairs, blades green above but suffused red-purple at margins and tip, blotched red-purple at tip, margins and in center of blade beneath, petioles about 6 mm long, the smaller leaves ovate, acuminate, serrate, about 10 mm long and 6 mm wide, green above, purple tipped beneath, vestiture as larger leaves. *Flowers* at least paired, bracts not seen; pedicels about

9 mm long, dull brown pilose; sepals lanceolate, acuminate, 3–4 toothed, teeth linear, to 3 mm long, sepals green, about 9 mm long and 1.5 mm wide at middle, externally dull brown pilose; corollas tubular, slightly zygomorphic, yellow with lower parts of the lobes red (producing a red ring around the dissected part of the corolla), about 4.6 cm long, about 3 mm in diameter at base becoming about 7 mm in diameter in middle then 5.5 mm in diameter at throat, lobes slightly unequal, lobed portion 6 mm long, spreading, corolla externally dull brown pilose, filaments remotely pilose at base otherwise glabrous, yellow, anthers included, 1 mm long and 1.5 mm wide, style glabrous, yellow, stigma not seen, ovary pilose, disk gland bilobed, fruits not seen.

Holotype: PANAMA. PROV. PANAMÁ: Cerro Jefe summit, altitude 2900 feet, *Dwyer et al.* 7235, March 12, 1967 (MO).

Columnea cruenta is not to be confused with *C. pectinata* Morton which has somewhat similar leaf coloration, but differently colored and shaped corollas, which place *C. pectinata* in sect. *Collandra*. *Columnea cruenta* is most closely related to *C. perpulchra* but differs in a number of characters, the most easily seen being the possession of red hirsute stems, shorter sepals and a more dense vestiture in all parts.

16. **Columnea segregata** sp. nov. (Sect. *Collandra*)

A *Columnea florida* Morton differt foliis brevioribus, sepalorum dentibus longioribus, et sepalorum pilis rubellis; a *Columnea serrata* (Kl. *ex.* Oerst.) Hanstein differt corollis tubiformibus pro parte majore flavis, et foliis inferioribus maculis rubris notatis.

Differing from *Columnea florida* Morton by the shorter leaves, longer sepal teeth, and reddish sepal hairs; differing from *Columnea serrata* (Kl. *ex* Oerst.) Hanstein notably by the tubular mainly yellow corolla and red blotched leaves.

Woody *herbs*, epiphytic, stems 4–5 mm in diameter, brown-purple villous. *Leaves* of a pair unequal, the larger lanceolate, abruptly acuminate, oblique at base, serrulate-crenulate, 11.3–13.6 cm long and about 3.5 cm wide at widest point, adaxially glabrous, abaxially sericeo-strigose, hairs 2–3-celled transparent adpressed, also 4–5-celled especially on veins, blades green above, red spotted or blotched to nearly concolorous beneath, petioles to 2 mm long, the smaller leaves lanceolate, acuminate, remotely serrate, 1.2–1.8 cm long and about 5 mm wide, green above and beneath, vestiture as larger leaves. *Flowers* solitary, bracteate, bracts 6–8 mm long, lanceolate, sericeo-strigose; pedicels about 2.3 cm long, transparent to reddish pilose; sepals pectinate, 6–7 toothed, teeth linear, to 6 mm long, sepals reddish, about 2 cm long and 2 mm wide excluding teeth at middle, externally reddish pilose; corollas tubular, slightly zygomorphic, yellow with reddish lobes, about 2 cm long when fully expanded, about 3 mm diameter at base, becoming about 5 mm in diameter at throat, lobes slightly unequal, lobed portion 2 mm long, spreading, corolla externally red pilose, filaments not seen, anthers included, style glandular papillose, stigma stomatomorphic, ovary pilose, disk gland not seen. *Fruit* about 7 mm in diameter (immature).

Holotype: PANAMA. PROV CHIRIQUÍ: Near Buena Vista, altitude 1500 feet (?), *Dressler s. n.*, December 2, 1964 (US). Topotype: *Butcher s. n.* (US).

Columnea segregata is close to *C. serrata* in all but corolla characters. The former has unusual small tubular corollas placing the species in sect. *Collandra*, while *C. serrata* has larger ventricose ones and is an *Ortholoma*.

17. The following sheets probably represent undescribed taxa, but inadequate material prevents formal description at the present.

Taxon 1. Sheets *Allen 1735* (MO) and *Hunter & Allen 566* (MO), both from Prov. Coclé, belong to a taxon related to *C. oerstediana*. The pedicels and almost linear sepals of immature flowers are red pilose.

Taxon 2. Sheet *Duke & Elias 13774* (MO) from Prov. Darién may be a new species in sect. *Collandra*. The reddish sepals are spathulate and the pilose leaves are concolorous red beneath. Corollas are needed.

Taxon 3. Sheets *Duke & Correa 14707*, *14707(4)*, and *14696(1)* (all MO) all belong to the same taxon from Prov. Coclé. Its sessile flowers are clustered in leaf axils and have pointed sepals, while the stems and leaves are coarsely pilose. Corollas are needed.

Sheet *Bristan 472* may be an atypical specimen of *C. nicaraguensis*, with very small linear lanceolate leaves, small sparsely sericeous corollas and small sepals. It is from Cerro Pirre in Prov. Darién, and more material would be welcome.

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ANNOTATED BIBLIOGRAPHY OF GALÁPAGOS BOTANY, 1836–1971[1]

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ABSTRACT

A bibliography of 286 annotated references concerning Galápagos botany has been assembled. The references cited are those which deal primarily or wholly with Galápagos plants and those of a more general nature which contain significant data or notes of historical value about Galápagos plants.

The Galápagos Islands, situated on the equator 600 miles west of Ecuador, have been the objects of botanical exploration and investigation since 1825. Many of the publications resulting from this work are obscure, and valuable bits of information about plants are hidden in papers dealing mainly with birds or animals. As I compiled references for my own use, I became aware of the need for one readily available listing of all pertinent material for Galápagos botanists.

This bibliography contains 286 references, arranged alphabetically by author under major plant groups. Such organization necessitates the repetition of some entries, but allows the reader to easily consult one section at a time. The references included may be divided into the following categories: (1) articles and books dealing wholly or primarily with Galápagos plants; (2) old (usually nineteenth century) articles and books of historical value which may contain only short discussions of plants; and (3) popular or general scientific works containing significant data on Galápagos flora or vegetation. Not included are the many popular accounts that only briefly mention plants and the lengthy taxonomic papers in which one or two Galápagos species are described. The latter may be found in the new *Flora of the Galápagos Islands* (Wiggins & Porter, 1971). A few exceptions are made for the cryptogams which have been poorly studied. All references have been seen, except where noted. Citations are based on the listings in G. H. M. Lawrence *et al.* (editors), *Botanico-Periodicum-Huntianum*, Pittsburgh, 1968.

The official Spanish names of the islands are used throughout. Below is a list of the names of the major islands and their Spanish equivalents.

Abingdon	Pinta
Albemarle	Isabela
Barrington	Santa Fé
Bindloe	Marchena
Charles	Floreana or Santa Maria
Chatham	San Cristobal

[1] The research leading to the preparation of this bibliography was aided by National Science Foundation grants GB-4654, GB-7154, and GB-17501. I am grateful for the use of library facilities at The Ohio State University, Harvard University, and the Hispanic Society of America and for the help of D. M. Porter. This is Contribution 139 from the Charles Darwin Foundation for the Galápagos Islands.

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ANN. MISSOURI BOT. GARD. 60: 461–477. 1973.

Hood	Española
Indefatigable	Santa Cruz
James	San Salvador or Santiago
Narborough	Fernandina
S. Seymour	Baltra
Tower	Genovesa

In addition to the references listed in the bibliography, information has been obtained from the following sources:

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ALGAE

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CROSSLAND, C. 1927. The expedition to the South Pacific of the S. Y. "St. George." Marine ecology and coral formations in the Panama region, the Galápagos and Marquesas Islands, and the atoll of Napuka. Trans. Roy. Soc. Edinburgh 55(pt. 2): 531–554. 11 figs. 1 pl. [General discussion of seaweeds found near Santiago, Santa Cruz, and Isabela, including map.]

DAWSON, E. Y. 1957. Notes on eastern Pacific insular marine algae. Los Angeles County Mus. Contr. Sci. 8: 1–8. 4 figs. [Discusses a collection of 22 species from Isabela and Fernandina, including 6 new records for the Galápagos.]

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———. 1964. Marine algae of the Galápagos. Not. Galápagos. 4: 11–12. [Seaweed flora includes 300 species, about 40% endemic; limited number of species in most areas because of grazing pressure by marine animals.]

DROUET, F. 1936. Myxophyceae of the G. Allan Hancock Expedition of 1934, collected by Wm. R. Taylor. Univ. S. Calif. Publ., Hancock Pacific Exped. 3(2): 15–30. 2 pl. [Lists 9 species from the Galápagos; includes long discussion of *Johannisbaptista primaria*, concluding that it should stand as a valid name until further study is made.]

——— & W. A. DAILY. 1956. Revision of the coccoid Myxophyceae. Butler Univ. Bot. Stud. 12: 1–218. 377 figs. [Discusses history of classificiation, morphology, preservation, location of specimens; describes 7 Galápagos species collected from lagoons, salt pools and mangrove swamps.]

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FARLOW, W. G. 1902. Algae. *In* B. L. Robinson, "Flora of the Galápagos Islands." Proc. Amer. Acad. Arts 38(4): 89–99. [Lists 47 species in 4 families, including 3 new species.]

HENDEY, N. I. 1971. Some marine diatoms from the Galápagos Islands. Nova Hedwigia 22(1–2): 371–422. 32 figs. [The most complete treatment to date of Galápagos diatoms; descriptions of lesser known species, 3 new species, 1 new variety and 3 new combinations; excellent illustrations.]

LEMOINE, P. 1929. Les Corallinacées de l'archipel des Galápagos et du Golfe de Panama. Arch. Mus. Hist. Nat. 4: 37–88. 35 figs. 4 pl. [In French. Lists 24 species from the Galápagos, 17 of which are new; notes high degree of endemism and affinity to Antillian coralline algae.]

PATRICK, R. 1970. The diatom flora of some lakes of the Galápagos Islands. *In* J. Gerloff & B. J. Cholnoky (editors), "Diatomaceae II. Friedrich Hustedt Gebenkband." Nova Hedwigia 31: 495–510. 1 pl. [Discusses diatoms from Fernandina and Isabela; describes 8 new species and 3 new varieties.]

PICONNE, A. 1889. Nuove alghe del viaggio di circumnavigazione della "Vettor Pisani." Atti Reale Accad. Lincei, Mem. Cl. Sci. Fis., Ser. 4, 6: 10–63. [In Italian. Brief discussion of voyage followed by catalogue of algae arranged by family and a geographical listing; includes 11 species collected around Floreana.]

SETCHELL, W. A. 1937. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 34. Report on the Sargassums. Proc. Calif. Acad. Sci., Ser. 4, 22(5): 127–158. 6 pl. [Lists 8 Galápagos taxa, including 2 new species, 3 new combinations, 1 new form; for each there is description, illustration and lengthy discussion.]

——— & N. L. GARDNER. 1937. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 31. A preliminary report on the algae. Proc. Calif. Acad. Sci., Ser. 4, 22(2): 65–98. 23 pl. [Describes 14 new species and 4 new varieties collected by Howell.]

SILVA, P. C. 1966. Status of our knowledge of the Galápagos benthic marine algal flora prior to the Galápagos International Scientific Project. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 149–156. [Discusses exploration and flora of 311 species of algae, 36% of which are endemic; tables show phycological exploration and a complete list of algae organized by order and family, with distributions.]

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FUNGI

ANDERSSON, N. J. 1855. Enumeratio plantarum in Insulis Galapagensis hucusque observatarum. Kongl. Vetensk. Akad. Handl. 1853: 123–256. [In Latin. One fungus, *Schizophyllum commune*, reported from Floreana.]

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LICHENS

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LINDER, D. H. 1934. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 8. Lichens. Proc. Calif. Acad. Sci., Ser. 4, 21(8): 211–224. 1 fig, 1 pl. [Lists 3 Galápagos species; one new combination made and illustrated.]

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Hepaticae

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Andersson, N. J. 1855. Enumeratio plantarum in Insulis Galapagensis hucusque observatarum. Kongl. Vetensk. Akad. Handl. 1853: 123–256. [In Latin. Lists 6 species of *Jungermannia* from Floreana.]

Bartram, E. B. & S. Arnell. 1961. Bryophytes of the Galápagos Islands collected principally by Gunnar Harling in 1959. Bryologist 64: 248–250. [Lists 34 species, 13 of which are new records for the islands, with distributions; one new combination described.]

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———. 1916. A new species of *Metzgeria* from the Galápagos Islands. Torreya 16: 67–70. 1 fig. [Describes the first species of this group of liverworts from the islands.]

Hooker, J. D. 1847. An enumeration of the plants of the Galápagos Archipelago, with descriptions of those which are new. Trans. Linn. Soc. London 20 (pt. 2): 163–233. [Lists 6 species of *Jungermannia*.]

Howe, M. 1934. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 17. The Hepaticae (chiefly *Riccia* and Anthocerotaceae) of the Galápagos Islands and the coast and islands of Central America and Mexico. Proc. Calif. Acad. Sci., Ser. 4, 21(17): 199–210. 1 pl. [Lists 3 species of *Riccia*, 2 of them new, and 3 new species of Anthocerotaceae.]

Robinson, B. L. & J. M. Greenman. 1895. On the flora of the Galápagos Islands, as shown by the collections of Dr. G. Baur. Amer. Jour. Sci. 50: 135–149. [Describes 1 species of *Frullania* from San Cristobal.]

Rose, J. N. 1892. List of plants collected by the U.S.S. *Albatross* in 1887–91 along the western coast of America. 2. List of plants from the Galápagos Islands. Contr. U. S. Natl. Herb. 1: 136–138. [Notes 1 species of *Plagiochila* growing on roots of *Parkinsonia*.]

Weber, W. A. 1966. Lichenology and bryology in the Galápagos Islands, with check lists of the lichens and bryophytes thus far reported. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 190–200. [Lists 70 species of liverworts in 11 families; some information on distribution and habitat; notes mats of *Marchantia* in upland areas are evidence of fire.]

Musci

Ångström, J. 1873. Förtekning och beskrifning öfner mossor, samlade af N. J. Andersson under Fregatten Eugenies verldsomseling åren 1851–1853. Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 30(5): 113–151. [In Latin. Lists 2 species of mosses from Floreana, 1 a new species with description.]

———. 1876. Fortsättning i öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar. 1873. No. 5. Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 52. [In Latin. Reports one name change for a moss included in above article.]

Andersson, N. J. 1855. Enumeratio plantarum in Insulis Galapagensis hucusque observatarum. Kongl. Vetensk. Akad. Handl. 1853: 123–256. [Lists 4 species of mosses.]

Bartram, E. B. 1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 8. Mosses of the Templeton Crocker Expedition, collected by John Thomas Howell and lists of the mosses known from the Galápagos and from Cocos Islands. Proc. Calif. Acad. Sci., Ser. 4, 21(8): 75–86. 3 figs. [Lists 18 species collected by Howell, 2 of which are new, and 14 additional species; 9 new records for islands.]

———. 1935. Musci. *In* H. K. Svenson, "Plants of the Astor Expedition, 1930 (Galápagos and Cocos Islands)." Amer. Jour. Bot. 22: 221. [Lists 2 species from Santa Cruz.]

———. 1948. Mosses collected by Dr. John Ericksson during the Swedish 'Albatross' Expedition 1947–48. Acta Horti Gothob. 18: 267–273. [Lists one species from the Galápagos.]

——— & S. ARNELL. 1961. Bryophytes of the Galápagos Islands collected principally by Gunnar Harling in 1959. Bryologist 64: 248–250. [Lists 10 species of mosses, 1 of which is new, with distributions.]

FARLOW, W. G. 1902. Musci. *In* B. L. Robinson, "Flora of the Galápagos Islands." Proc. Amer. Acad. Arts 38(4): 102–104. [Lists 9 species, none new; lengthy description and discussion of *Campylopus lamellatus*.]

HOOKER, J. D. 1847. An enumeration of the plants of the Galápagos Archipelago, with descriptions of those which are new. Trans. Linn. Soc. London 20 (pt. 2): 163–233. [Lists 2 species, one of which is new.]

MÜLLER, K. 1856. Om Galápagos-öarnes vegetation, af N. J. Andersson. Stockholm, 1854, bei P. A. Norstedt et Söner. Bot. Zeit. 14: 167–171. [In German. Primarily a review of Andersson's publication (above) with discussion of mosses; 2 new species and one other species described.]

STEERE, W. C. 1936. Mosses of the G. Allan Hancock Expedition of 1934, collected by Wm. R. Taylor. Univ. S. Calif. Publ., Hancock Pacific Exped. 3(1): 1–12. 1 pl. [Lists 11 Galápagos species in 8 families, including 1 new species and 5 new records.]

———. 1948. Contributions to the bryogeography of Ecuador. I. A review of the species of Musci previously reported. Bryologist 51: 65–167. [Lists 47 families of which 12 have Galápagos representatives totalling 29 species; one new combination.]

WEBER, W. A. 1966. Lichenology and bryology in the Galápagos Islands, with check lists of the lichens and bryophytes thus far reported. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 190–200. [Lists 39 species in 16 families; some information on distribution and habitat, noting abundance of mosses in forest zone and *Sphagnum* in grassland pools.]

WILLIAMS, R. S. 1924*a*. Galápagos and Cocos Island mosses collected by Alban Stewart in 1905–6. Bryologist 27: 37–45. 4 pl. [Reports 17 mosses collected by Stewart and mentions 6 others; one new species described from San Cristobal.]

———. 1924*b*. Note on Galápagos and Cocos Island mosses. Bryologist 27: 65. [Adds 3 species omitted above, 2 from Galápagos.]

PTERIDOPHYTA

ACOSTA SOLIS, M. 1937. Galápagos observado fitologicamente. Univ. Central, Quito. 78 pp. 30 pl. [In Spanish. Reports a collection of 27 ferns, no descriptions.]

ANDERSSON, N. J. 1855. Enumeratio plantarum in Insulis Galapagensis hucusque observatarum. Kongl. Vetensk. Akad. Handl. 1853: 123–256. [In Latin. Lists 31 species; describes 2 new species and records collection of *Azolla* in cold springs on Floreana.]

CARUEL, T. 1889. Contribuzione alla flora delle Galápagos. Rendiconti Acad. Lincei 5(pt. 1): 619–625 [In Italian. Lists 4 ferns collected on voyage of "Vettor Pisani."]

CHRISTOPHERSEN, E. 1931. A collection of plants from the Galápagos Islands. Nyt. Mag. Naturvidensk 70: 67–95. 1 pl. [Lists 17 species of ferns and *Lycopodium*, including 4 new records, collected by Miss Rorud, 1927–29.]

GALLEGOS TERAN, J. A. 1945. Inventario floristico de algunas islas del Archipiélago de Colón. Bol. Inst. Bot. Univ. Central 4(5): 155–166. 7 pl. [In Spanish. Lists 16 ferns and fern allies from San Cristobal and Isabela with brief descriptions and notes on habitat.]

HOOKER, J. D. 1847. An enumeration of the plants of the Galápagos Archipelago, with descriptions of those which are new. Trans. Linn. Soc. London 20 (pt. 2): 163–233. [Lists 27 species, 7 of which are new.]

JARRETT, F. M., I. MANTON & S. K. ROY. 1968. Cytological and taxonomic notes on a small collection of living ferns from Galápagos. Kew Bull. 22(3): 475–480. 2 pl. [Fern rhizomes studied; 15 species representing 11 genera are discussed; table summarizes chromosome counts.]

MOMOSE, S. 1965*a*. Prothallia of some ferns from the Galápagos Islands (1). Jour. Jap. Bot. 40(5): 140–147. 7 figs. [Describes and illustrates prothallia of 3 ferns.]

———. 1965*b*. Prothallia of some ferns of Galápagos Islands (2). Jour. Jap. Bot. 40(9): 277–281. 4 figs. [Describes and illustrates 2 additional prothallia.]

MORTON, C. V. 1957. Ferns of the Galápagos Islands. Leafl. W. Bot. 8(8): 188–195. 2 pl. [Describes species in 12 genera not included in Svenson (1938) or incorrectly

determined, including new species, *Hemitelia weatherbyana*, and 2 new combinations; key to 4 species of *Elaphoglossum*.]

———. 1969. New combinations in *Cyathea*, *Ctenitis* and *Asplenium*. Amer. Fern Jour. 59(2): 65–67. [One new Galápagos combination in each of 3 genera including change of *Hemitelia* to *Cyathea*].

Riley, L. A. M. 1925. Critical notes on Galápagos plants ("St. George" Pacific Expedition, 1924). Bull. Misc. Inform. 1925(5): 216–231. [First record of *Psilotum* in the Galápagos.]

Robinson, B. L. 1902. Flora of the Galápagos Islands. Proc. Amer. Acad. Arts 38(4): 77–270. [Lists 65 species of ferns, none new, and 2 species of *Lycopodium*.]

——— & J. M. Greenman. 1895. On the flora of the Galápagos Islands, as shown by the collections of Dr. G. Baur. Amer. Jour. Sci. 50: 135–149. [Lists 15 species of ferns, 7 of which are new records, and reports *Lycopodium* for the first time.]

Schofield, E. K. & P. A. Colinvaux. 1969. Fossil *Azolla* from the Galápagos Islands. Bull. Torrey Bot. Club 96(6): 623–628. 2 figs. [The first record of fossil fern spores from the Galápagos; *A. filiculoides* spores are found in lake sediments older than 48,000 years B.P. and *A. microphylla* spores from 10,000 years B.P. to present.]

Stewart, A. 1911. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906. II. A botanical survey of the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4, 1: 7–288. 34 pl. [Lists 83 species of ferns and fern allies, with some notes on habitat.]

Svenson, H. K. 1938. Pteridophyta of the Galápagos and Cocos Islands. Proc. Calif. Acad. Sci. 65: 303–333. 3 pl. [Lists 25 species of ferns, 2 of which are new, one *Equisetum*, one *Lycopodium*, and 1 *Psilotum*.]

———. 1944. The New World species of *Azolla*. Amer. Fern Jour. 34(3): 69–84. 3 pl. [Discusses life cycle, history, and distribution of *Azolla*; *A. microphylla* from Galápagos is described and illustrated.]

———. 1946. Vegetation of the coast of Ecuador and Peru and its relation to that of the Galápagos Islands. II. Catalogue of plants. Amer. Jour. Bot. 33(6): 427–498. [Lists 8 species of ferns.]

Wiggins, I. L. & D. M. Porter. 1971. Flora of the Galápagos Islands. Stanford Univ. Press, Stanford, Calif. 998 pp. 268 figs. 96 pls. [Descriptions, synonymy, notes on habitat, distribution maps, and illustrations for 89 species of ferns and fern allies, 15 of which are new records.]

Spermatophyta

Acosta Solis, M. 1937. Galápagos observado fitologicamente. Univ. Central, Quito. 78 pp. 30 pl. [In Spanish. Discusses agriculture, factors influencing vegetation, biology of plants; describes dry and moist zones, with map showing their approximate areas on all islands; lists a collection of 200 plants.]

Agassiz, A. 1892. Reports on the dredging operations off the west coast of Central America to the Galápagos, etc. by the U.S. Fish Commission steamer "Albatross." II. General sketch of the expedition of the "Albatross" from February to May, 1891. Bull. Mus. Zool. 23: 1–89. 22 pl. [Describes vegetation zones and discusses vegetation of San Cristobal and Floreana in general terms.]

———. 1895. Cactaceae in the Galápagos Islands. Nature 53: 199. [A comment on a publication by Hemsley (1895*b*) denying that Baur was with the *Albatross* Expedition and noting that Agassiz collected cacti on the islands and Wolf described *Cereus* and *Opuntia*.]

Anderson, E. A. [=E. F. Anderson]. 1966. Cacti seen on Galápagos Islands. Shaboten 61: 8–13. 28 pl. [In Japanese. Discusses several species and varieties of cacti observed on various islands; illustrated with photographs, captions in Japanese.]

Anderson, E. F. 1967*a*. An account of my cactus collecting trip to the Galápagos Islands. Cact. Succ. Jour. (Los Angeles) 39(5): 186–199. 28 figs. [Popular discussion of cacti seen on nearly every island; no descriptions of plants given.]

———. 1967*b*. Bericht über meine Kakteen Sammelreise nach den Galápagos Inseln. Kakteen Sukk. 8: 147–155. [In German. Not seen.]

———. 1969. *Opuntia echios*. Bio Science 19(12). Cover photograph and caption. [A giant prickly pear cactus with a trunk 40 inches in diameter, photographed on Santa Fé.]

——— & D. L. Walkington. 1967. A study of some neotropical opuntias. I. Ecology and morphology. Amer. Jour. Bot. 54 (5, pt. 2): 645. Abstract. [Studies show tendency toward morphological diversity in Galápagos species; little relation to species of Ecuador.]

——— & ———. 1968. A study of some neotropical opuntias of coastal Ecuador and the Galápagos Islands. Not. Galápagos 12: 18–22. 4 figs. [Morphological and chemical studies show little relation between cacti of Ecuador and Galápagos.]

——— & ———. 1970. New combinations and taxa in the Cactaceae of the Galápagos Islands. Madroño 20(5): 256. [Discusses 2 varieties each of *Jasminocereus* and *Opuntia*, one of which is new.]

ANDERSSON, N. J. 1855*a*. Om Galápagos-öarnes vegetation. Kongl. Vetensk. Akad. Handl. 1853: 61–120. [In Swedish. Reviews other expeditions; describes vegetation of 5 islands; discusses 13 largest families represented on islands and relationship of flora to that of South America, Mexico, etc. According to Svenson (1935) a publication of the same name, dated 1857, is a reprint of this paper, with a few changes. The list of plant names associated with it was not published until 1861. Not seen.]

———. 1855*b*. Enumeratio plantarum in Insulis Galapagensis hucusque observatarum. Kongl. Vetensk. Akad. Handl. 1853: 123–256. [In Latin. Lists 57 families, 166 genera (3 new) and 343 species (75 new).]

———. 1861. Ueber die vegetation der Galápagos-Inseln. Linnaea 31: 571–631. [In German. Discussion of vegetation of 5 islands, including characteristic plants, geographic affinities and origin of vegetation.]

BACIGALUPI, R. 1931. Taxonomic studies in *Cuphea*. Contr. Gray Herb. 95: 3–26. [A note that Stewart's specimens from the Galápagos were wrongly named *C. patula* and should be assigned to *C. carthagenensis*.]

BALGOOY, M. M. J. VAN. 1960. Preliminary plant-geographical analysis of the Pacific. Blumea 10(2): 385–430. [Analyzes Galápagos flora on basis of 9 types of geographical distributions, finding over 50% of genera to be worldwide and 40% to be tropical or subtropical American genera.]

BAUR, G. 1891. On the origin of the Galápagos Islands. Amer. Naturalist 25: 217–229, 307–319. [Includes a general description of flora and outline of vegetation zones.]

———. 1892. Ein besuch der Galápagos-Inseln. Biol. Centralbl. 12: 221–250. [In German. A general article, including some discussion of plants, *e.g.* the distribution of tall and short *Opuntia* on various islands.]

BENTHAM, G. 1871–73. Notes on the classification, history and geographical distribution of Compositae. Jour. Linn. Soc., Bot. 13: 335–577. 4 pl. [A table lists 18 genera and 27 endemic species from the Galápagos and shows geographical affinities; notes that Galápagos Compositae do not show arborescent tendency.]

BLAKE, S. F. 1921. Revision of the genus *Acanthospermum*. Contr. U. S. Natl. Herb. 20: 380–392. 1 pl. [Discusses *A. lecocarpoides* from the Galápagos and notes how it can be distinguished from *Lecocarpus*.]

———. 1922. Two new species of *Acanthospermum* from the Galápagos Islands. Jour. Wash. Acad. Sci. 12(8): 200–205. 1 fig. [Describes species based on Stewart specimens from San Cristobal and Gardner; discusses relationship of genus to *Melampodium*.]

BORGER, S. C. 1968. A test for resistance to *Fusarium* wilt of tomato in *Lycopersicon* sp., a wild species from the Galápagos Islands. Unpublished manuscript. Allegheny College. [Galápagos species is not resistant to wilt.]

BOWMAN, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. Univ. Calif. Publ. Zool. 58: 1–302. 74 figs. 22 pl. [Discusses composition of flora, with a table comparing various islands; outlines vegetation zones of Santa Cruz indicating percent area of island covered by each.]

———. 1963. Evolutionary patterns in Darwin's finches. Occas. Pap. Calif. Acad. Sci. 44: 107–140. 20 figs. [General description of vegetation zones illustrated by diagrammatic drawing of those on Santa Cruz and several photographs.]

——— (editor). 1966. The Galápagos. 318 pp. Univ. Calif. Press, Berkeley and Los Angeles. [Several chapters on Galápagos plants; listed here by author.]

BRITTON, N. L. 1924. Plants of the Galápagos Islands. Jour. New York Bot. Gard. 25: 10–11. [Adds 5 new records to flora from collection of Williams Expedition.]

BURCH, D. 1969. Notes on the Galápagos Euphorbieae (Euphorbiaceae). Ann. Missouri Bot. Gard. 56(2): 173–178. 2 figs. [Plants formerly known as *Euphorbia* are transferred to *Chamaesyce*; 7 new combinations and one new species are described; key to 10 species provided.]

———. 1970. A new combination in *Chamaesyce* from the Galápagos Islands. Madroño 20(5): 253. [*C. nummularia* var. *glabra* from Floreana.]

CARLQUIST, S. 1965. Island Life. Natural History Press, Garden City, New Jersey. 451 pp.

[A chapter on the Galápagos includes a brief description of vegetation zones, discussion of endemic cacti and *Scalesia*, the latter with a useful map showing island distribution of species with leaf and flower of each pictured.]

———. 1966. The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. Evolution 20(1): 30–48. 7 figs. [Discusses endemic Galápagos Compositae, noting loss of means of dispersal or maintenance of mechanisms suited only to short-distance dispersal.]

———. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. Bull. Torrey Bot. Club. 94: 129–162. 13 figs. [A chart shows modes of dispersal of Galápagos plants; rafting is least common; transport by birds is most common.]

Caruel, T. 1889. Contribuzione alla flora delle Galápagos. Rendiconti Acad. Lincei 5(pt. 1): 619–625. [In Italian. A catalogue of 43 plants collected on the voyage of the "Vettor Pisani" in 1884, including some cultivated plants; 2 new species described.]

Cavagnaro, D. 1965. Exploring the Galápagos on foot. Pacific Disc. 18 (5): 14–22. 18 figs. [Popular account, including descriptions of vegetation of Darwin, Wolf, Fernandina and Santa Cruz; photographs of *Scalesia*, *Cyathea*, and *Sphagnum* bogs.]

Christophersen, E. 1931. A collection of plants from the Galápagos Islands. Nyt. Mag. Naturvidensk 70: 67–95. 1 pl. [Lists plants collected by Miss Rorud, 1927–29: 138 species, including 10 new records and 2 new species.]

Colinvaux, P. A. 1969*a*. Analyse du pollen de Galápagos: histoire d'une flore epargnée par l'influence de l'homme. VIII INQUA Congr. (Paris), Résumés Commun., p. 79. [Abstract, in French. Discusses pollen analysis of lake sediments to seek changes in Galápagos vegetation before man's influence.]

———. 1969*b*. Vegetation of a Galápagos island before and after an ice age. Ann. Missouri Bot. Gard. 56: 419. [Changes in vegetation and climate are indicated by pollen content of lake sediments from San Cristobal.]

———, E. K. Schofield & I. L. Wiggins. 1968. Galápagos flora: Fernandina (Narborough) caldera before recent volcanic event. Science 162: 1144–1145. [Discusses a collection of plants from an inner cone of the caldera and the probable effects of the 1968 eruption; table shows Galápagos distribution of species.]

Cronquist, A. 1970. New combinations in the Compositae of the Galápagos Islands. Madroño 20(5): 255–256. [5 new combinations and one new record for islands; changes *Acanthospermum* to *Lecocarpus*.]

Darwin, C. 1913. A Naturalist's Voyage Round the World (Journal of Researches. . . .). John Murray, London. 551 pp. [Discusses distribution of flora; chart shows distribution of Leguminosae; sketch of *Opuntia galapageia*, which is unique to this edition.]

Dawson, E. Y. 1962*a*. Cacti of the Galápagos Islands and of coastal Ecuador. Cact. Succ. Jour. (Los Angeles) 34(3): 67–74. 5 figs. 34(4): 99–105. 6 figs. [Description of cacti with keys to Galápagos species, including one new species and 5 new varieties.]

———. 1962*b*. The giants of Galápagos. Nat. Hist. 71(9): 52–57. 9 figs. [General discussion of cacti, their origin and growth forms.]

———. 1962*c*–1964. Field Notes. Unpublished manuscripts, Smithsonian Institution. [Notes mainly concerning Galápagos cacti, including morphology, distribution, flowering time; lists of species collected.]

———. 1963. Additional note on *Jasminocereus howellii*. Cact. Succ. Jour. (Los Angeles) 35(2): 42. 1 pl. [Photographs illustrating long spines and small, short flowers typical this species.]

———. 1964. Cacti in the Galápagos Islands. Not. Galápagos 4: 12–13. [Reviews previous work; discusses relation of tortoise grazing to growth form of *Opuntia*.]

———. 1965*a*. An undescribed *Melocatus*? in the Galápagos Islands. Cact. Succ. Jour. (Los Angeles) 37(5): 126. [Discusses search for a globular cactus reported from Santa Cruz.]

———. 1965*b*. Further studies in *Opuntia* in the Galápagos Archipelago. Cact. Succ. Jour. (Los Angeles) 37(5): 135–148. 18 figs. [Notes that *Opuntia* shows trend of evolution from low-growing to arborescent in response to tortoise foraging and returns to low form when this pressure is removed.]

———. 1966. Cacti in the Galápagos Islands, with special reference to their relations with tortoises. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 209–214. [Further discussion of growth forms, review of other collections and relationships of cacti.]

Douglas, D. 1836. A sketch of a journey to the north-western parts of the continent of

North America, during the years 1824, 5, 6 and 7. Companion Bot. Mag. 2: 82–105. [Brief description of plants seen on Santiago, discussed more fully in his journal, below.]

———. 1914. Journal kept by David Douglas during his Travels in North America 1823–1827 . . . W. Wesley and Son, London. 364 pp. [The first botanist to visit the Galápagos briefly discusses flora and mentions a collection of 175 plants from Santiago, most of which were lost.]

DU PETIT-THOUARS, A. 1841. Voyage autour de monde sur la frégate *La Vénus* pendant les années 1836–1839. . . . Vol. 2. Gide, Paris. 464 pp. [In French. Discusses vegetation of nearly every island, with most detail about Floreana; non-technical descriptions of 3 types of cacti and other plants.]

ELIASSON, U. 1965*a*. Studies in Galápagos plants. I. Leguminosae. Svensk Bot. Tidskr. 59(3): 345–367. 8 figs. [Discusses 23 species and lists 10 new records for the islands.]

———. 1965*b*. Studies in Galápagos plants. II. Cyperales. Svensk Bot. Tidskr. 59(4): 469–491. 4 figs. [Describes 25 species, 5 of which are new to the islands, and notes additional species reported from Galápagos but not seen.]

———. 1966. Studies in Galápagos plants. III. Centrospermae. Svensk Bot. Tidskr. 60(3): 393–439. 15 figs. [Discussion of 40 species in 9 families, including 2 new records.]

———. 1967. Studies in Galápagos plants. IV. The genus *Chrysanthellum*. Svensk Bot. Tidskr. 61(1): 88–92. 2 figs. [2 endemic species, one new, are described and discussed.]

———. 1968*a*. On the influence of introduced animals on the natural vegetation of the Galápagos Islands. Not. Galápagos 11:19–21. [Cites several examples of damage done by goats, *e.g.* 3 species of *Scalesia* on Santiago have nearly been wiped out; notes distribution of some plants (*e.g. Portulaca*) is limited to smaller islands where there are no introduced animals.]

———. 1968*b*. Studies in Galápagos plants. V. Some new botanical records from the archipelago. Svensk Bot. Tidskr. 62(1): 243–248. 1 fig. 2 pl. [Describes 4 plants collected for the first time in 1966–67.]

———. 1968*c*. Studies in Galápagos plants. VI. On the identity of *Calandrinia galapagosa* St. John. Svensk Bot. Tidskr. 62(2): 365–368. 2 figs. 1 pl. [Describes the species, giving its history and distribution.]

———. 1968*d*. Studies in Galápagos plants. VII. On some new or noteworthy plants from the archipelago. Bot. Not. 121: 630–640. 5 figs. [Describes 2 new species of *Linum*; lists 2 new records and extends distribution of *Ophioglossum*.]

———. 1970*a*. Studies in Galápagos plants. VIII. Chromosome numbers of some endemic species. Bot. Not. 123: 149–154. 1 fig. [Discusses and illustrates chomosomes of *Nolana*, *Pleuropetalum*, *Lecocarpus*, and several species of *Scalesia*.]

———. 1970*b*. Studies in Galápagos plants. IX. New taxonomical and distributional records. Bot. Not. 123: 346–357. 5 figs. [Lists 4 plants new to islands, extends distribution among islands of 3 species; includes distribution map for *Nolana*.]

———. 1970*c*. Nomenclatural changes and new subspecies in the Centrospermae of the Galápagos Islands. Madroño 20(5): 264–266. [Makes 5 new combinations in Amaranthaceae, Aizoaceae and Basellaceae.]

———. 1971. Studies in Galápagos plants. X. The genus *Lecocarpus* Decaisne. Svensk Bot. Tidskr. 65: 245–277. 18 figs. [Discusses taxonomy, ecology, dispersal mechanisms, wood anatomy, cytology and embryology of this endemic genus.]

ERNST, W. R. 1971. Flora of the Galápagos Islands. Madroño 21: 111–112. [A review of Wiggins and Porter, entry below.]

FOSBERG, F. R. 1967. Observations on vegetation patterns and dynamics on Hawaiian and Galápageian volcanoes. Micronesica 3: 129–134. [Describes vegetation of Fernandina, including a new record, *Sonchus*.]

GALLEGOS TERAN, J. A. 1945. Inventario floristico de algunas islas del Archipiélago de Colón. Bol. Inst. Bot. Univ. Centr. 4(5): 155–166. 7 pl. [In Spanish. Lists 103 flowering plants from 5 islands; brief descriptions and notes on habitat.]

HAGEN, W. VON. 1937. The Galápagos Islands. Proc. Linn. Soc. London 149(2): 99–103. [General descriptions of vegetation zones, mentioning poisonous tree (*Hippomane*) and introduction of cultivated plants.]

HAMILTON, T. H., I. RUBINOFF, R. H. BARTH, JR. & G. L. BUSH. 1963. Species abundance: natural regulation of insular variation. Science 142: 1575–1577. 2 figs. [Discusses a theory of predicting numbers of plant species on islands in the Galápagos based on elevation, area of the adjacent island, distance from nearest island and distance from center of archipelago.]

HARLING, G. 1962. On some Compositae endemic to the Galápagos Islands. Acta Horti Berg. 20(3): 63–120. 25 figs. 8 pl. [Reviews morphology, embryology, nomenclature, and distribution of *Scalesia*, *Macraea*, and *Darwiniothamnus*, a new genus; describes 2 new species and provides key to species of *Scalesia*.]

———. 1964. Galápagos oarna ett botaniskt isolat. Bot. Gothob. 11: 3–20. [In Swedish. Not seen.]

HÄSSLER, A. 1939. On the limitation of the species within the *Euphorbia*-group Cheloneae Boiss. Preliminary note. Bot. Not. 1939: 745–748. [Except for one species, this group is confined to Galápagos; divides into 2 sub-groups on basis of smooth or hairy seeds; discusses latter type and reduces 4 species to synonymy.]

HEMSLEY, W. B. 1885. Report on present state of knowledge of various insular floras, being an introduction to the first three parts of the botany of the *Challenger* Expedition. *In* "Report on the scientific results of the voyage of the H. M. S. *Challenger* during the years 1873–76." Botany I: 1–72. Neill and Co., Edinburgh. [Reports 332 species of flowering plants have been collected from 5 of the Galápagos Islands; notes that families such as Compositae, Rubiaceae, Euphorbiaceae and Amaranthaceae are represented by many endemics.]

———. 1894. Insular floras. Part II. Sci. Progr. (London, 1894–1900) 1: 387–404. [Criticizes recent expeditions (*Vettor Pisani* and *Albatross*) for failing to record new plants from the Galápagos; mentions vegetation zones; lengthy bibliography.]

———. 1895*a*. The flora of the Galápagos Islands. Nature 52: 623. [Discusses botanical evidence for Baur's subsidence theory, noting widespread genera that have endemic species confined to one island.]

———. 1895*b*. Cactaceae in the Galápagos Islands. Nature 53: 31. [Notes the unusual cacti and their importance to animals as a source of moisture.]

———. 1895*c*. Cactaceae in the Galápagos. Nature 53: 249. [Letter apologizing for wrongly connecting Baur with the *Albatross* Expedition, but noting that he has photographs of cacti taken by Baur (see Agassiz, 1895).]

———. 1896. Insular floras. Part VI(A). Sci. Progr. (London, 1894–1900) 5: 286–303. [Notes that Compositae are characteristic of volcanic islands like the Galápagos, discusses misconception of large endemic content of flora; several genera reduced to synonymy.]

———. 1898. The Cactaceae of the Galápagos Islands. Gard. Chron., Ser. 3. 24: 265. 1 fig. [Discussion of Baur's (and others') writings about cacti; description and photograph of *Opuntia galapageia*.]

———. 1900*a*. The vegetation of the Galápagos Islands. Gard. Chron., Ser. 3. 27: 177–178. 2 figs. [Discusses vegetation of 300 species of flowering plants, especially Cactaceae; brief description of 3 vegetation zones.]

———. 1900*b*. The Cactaceae of the Galápagos Islands. Gard. Chron., Ser. 3. 28: 7–8. [Notes that David Douglas, on Santiago in 1825, collected seeds of a large *Opuntia* apparently not observed by others.]

———. 1900*c*. *Opuntia myriacantha*. Gard. Chron., Ser. 3. 28: 220. [Weber suggests that plant collected by Douglas (above) was *O. myriacantha*.]

———. 1902. The flora of the Galápagos Islands. Gard. Chron., Ser. 3. 32: 469. [Briefly describes vegetation zones, endemics, new species of Robinson; mentions monocots from islands and recent collections, including water plants; notes that Cactaceae are only Galápagos plants of horticultural interest.]

———. 1905. *Scalesia retroflexa* Hemsl., *S. incisa* Hook. f., *S. pedunculata* Hook. f., *S. affinis* Hook. f., *S. darwinii* Hook. f. Hooker's Icones Plantarum, Ser. 4. 8: 2715–2719. [Brief descriptions, notes on locality and collector accompanying illustrations.]

HENSLOW, J. S. 1837. Description of two new species of *Opuntia*; with remarks on the structure of the fruit of *Rhipsalis*. Mag. Zool. Bot. 1: 466–469. 2 figs. [Describes *O. galapageia*, tree cactus collected by Darwin on Santiago; also mentions *Cereus* as invader of new lava beds.]

HITCHCOCK, A. S. 1935. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 24. New species of grasses from the Galápagos and the Revillagigedo Islands. Proc. Calif. Acad. Sci., Ser. 4. 21(24): 295–300. [Discusses collection make by Howell; describes 3 new species and 1 new variety.]

HOOKER, J. D. 1846. Description of *Pleuropetalum*, a new genus of Portulacaceae, from the Galápagos Islands. London Jour. Bot. 5: 108–109. 1 pl. [Latin description of genus and 1 new species, *P. darwinii*, from Santiago. This genus is now placed in Amaranthaceae.]

———. 1847*a*. An enumeration of the plants of the Galápagos Archipelago, with descriptions

of those which are new. Trans. Linn. Soc. London 20 (pt. 2): 163–233. [Lists 21 species of monocots, 8 of which are described as new and 179 species of dicots, including 5 new genera and 91 new species; notable are the descriptions of many Euphorbiaceae and several species of *Scalesia*.]

———. 1847*b*. On the vegetation of the Galápagos Archipelago, as compared with that of some other tropical islands and of the continent of America. Trans. Linn. Soc. London 20(2): 235–262. [Discusses vegetation zones, composition and affinities of flora, means of dispersal and most important families; tables show distribution of species; addenda list collection by Edmonstone from Floreana and some corrections for Hooker's enumeration of flora, above.]

———. 1849. Enumeration of the plants of the Galápagos Islands, with descriptions of the new species. Proc. Linn. Soc. London 1: 276–279. [A review of previous paper (1847*a*) mentioning the number of plants described and repeating descriptions of 6 new genera.]

HOOKER, W. J. & G. A. W. ARNOTT. 1861. Contributions towards a flora of South America and the islands of the Pacific. Jour. Bot. 3: 310–348. [Latin description of genus *Scalesia* and one new species, *S. atractyloides*.]

HOWELL, J. T. 1933*a*. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 3. The genus *Mollugo* in the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 21(3): 13–23. [Discusses specialized Galápagos species and 2 lines of development; lists 8 species, 3 of which are new, and 8 subspecies, 7 of which are new; key to species provided.]

———. 1933*b*. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 5. The Cactaceae of the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 21(5): 41–54. 4 figs. [Lists 7 species, 3 of which are new, and 4 subspecies of *Opuntia*, with key, and 2 species of *Cereus*.]

———. 1933*c*. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 9. The Amaranthaceae of the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 21(9): 87–116. [Notes highly endemic development of this family; discusses 7 genera, 33 species, 2 of which are new, and numerous subspecies and forms; several keys provided.]

———. 1934*a*. Cacti in the Galápagos Islands. Cact. Succ. Jour. (Los Angeles) 5: 515–518. 4 figs. [Popular account of trip with Templeton Crocker Expedition, dealing mainly with *Opuntia*.]

———. 1934*b*. Cacti in the Galápagos Islands. Part II. Cact. Succ. Jour. (Los Angeles) 5: 531–532. 3 figs. [Continues the account with discussion of *Cereus*.]

———. 1934*c*. Concerning the names of the species of *Cereus* in the Galápagos Islands. Cact. Succ. Jour. (Los Angeles) 5: 585–586. [In answer to a letter from W. T. Marshall, the author defends his use of names *Cereus thouarsii* and *C. nesioticus* and concludes that there is not enough evidence to justify use of new names *Jasminocereus* and *Brachycereus*.]

———. 1935*a*. Sea-gulls and tarweeds: a distributional mix-up. Leafl. W. Bot. 1(16): 189–191. [Presents evidence that a record of *Hemizonia squalida* from Galápagos is erroneous; plant was probably a form of *H. angustifolia* collected in California.]

———. 1935*b*. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 26. New flowering plants from the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 21(26): 329–336. [Describes 6 new species in 5 families, includes key to species of *Pectis*.]

———. 1936. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 32. The plant genus *Coldenia* in the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 22(3): 99–110. 2 pl. [Reviews history of this genus on islands, discusses type specimens, ecology and relationships of genus; key to 4 species, 2 of which are described as new.]

———. 1941*a*. Hugh Cuming's visit to the Galápagos Islands. Lloydia 4: 291–292. [Date of visit not certain, probably 1829; Cuming collected specimens from which genus *Scalesia* was established.]

———. 1941*b*. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 40. The genus *Scalesia*. Proc. Calif. Acad. Sci., Ser. 4. 22(11): 221–271. [Discusses history, morphology, relationships, distribution; 19 species described, including one new species; key provided.]

———. 1942. Up under the equator. Sierra Club Bull. 27: 79–82. [General account of first ascent to the summit of Santa Cruz and first glimpse of upland vegetation, including tree ferns.]

———. 1957*a*. The 1932 Templeton Crocker Expedition, twenty-five years later. Leafl. W.

Bot. 8(8): 181–186. 2 pl. [Reviews collections, including 2555 vascular plants; photographs of fern-covered uplands of Santa Cruz; bibliography.]

———. 1957*b*. The *Atriplex* of the Galápagos Islands. Leafl. W. Bot. 8(8): 195–197. [Describes plant, lists collections, and tentatively assigns it to *A. peruviana* Moq.]

———. 1964. Serendipity *à la botanique*. Leafl. W. Bot. 10(7): 111–117. [Describes climb to the top of mountain peak east of Tagus Cove (Isabela), with some notes on vegetation.]

———. 1966. Plantae Galapaganae excerptae. Leafl. W. Bot. 10(16): 351–352. [Latin descriptions and discussion of 2 new varieties (in *Drymaria* and *Polygala*) and one new species (*Sesuvium*).]

——— & D. M. Porter. 1968. The plant genus *Polygala* in the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 32(19): 581–586. [Discusses 3 species and 4 varieties, with key, descriptions and distributions.]

Howmiller, R. & A. Weiner. 1968. A limnological study of a mangrove lagoon in the Galápagos. Ecology 49(6): 1184–1186. 3 figs. [Provides some ecological information about the waters surrounding *Rhizophora mangle* on Isabela.]

Itow, S. 1964. A record of expedition to Galápagos and Cocos Island. Hikobia 4: 110–124. 14 figs. [In Japanese. General discussion of vegetation on several islands, including San Cristobal and Española; photographs of several plants.]

———. 1965. Preliminary note on the vegetation of the Galápagos Islands, Ecuador. Hikobia 4(4): 318–323. 2 figs. [Distributional range of important trees studied in relation to percentage of lava substrate; DBH and height of trees measured.]

———. 1967. Ecological approaches to the vegetation of the Galápagos—future needs. Not. Galápagos 7/8: 10–12. [Mentions differences in vegetation zones on various islands, different habitats of several types of mangroves and stresses need for more detailed vegetation studies.]

———. 1971. A study of vegetation in Isla Santa Cruz, Galápagos Islands. Not. Galápagos 17: 10–13. 1 fig. [A rather detailed discussion of highland vegetation with a map; transects of vegetation on north and south sides of island; brief discussion of secondary communities.]

Johnston, I. M. 1924. Studies in the Boraginaceae. II. A tentative classification of the South American *Coldenias*. Contr. Gray Herb. 70: 55–61. [All Galápagos *Coldenias* belong to one variable species, *C. darwinii*, which is described.]

———. 1935. Studies in the Boraginaceae, XI. Jour. Arnold Arbor. 16(2): 145–205. [Describes 4 endemic species of *Cordia* from the Galápagos; key provided.]

———. 1936. A study of the Nolanaceae. Contr. Gray Herb. 112: 1–87. [Discusses relationships and distribution of family; makes a new combination, *N. galapagensis*, a littoral species of several islands.]

———. 1938. Notes on some *Astragalus* species of Ecuador and Peru. Jour. Arnold Arbor. 19: 88–96. [Confusion of specimens led to description of 2 species from the Galápagos which actually were not collected there (cf. Wright, 1906).]

Kastadalen, A. 1965. Changes in the biology of Santa Cruz Island during the last thirty years. Unpublished manuscript, Charles Darwin Station. [A resident of Santa Cruz describes changes in vegetation, especially *Miconia* and *Scalesia*, due to fire, drought and grazing by animals.]

Kearney, T. H. 1934. American wild cottons with thirteen chromosomes. Jour. Heredity 25: 305–312. 4 figs. [Discusses *Gossypium klotzschianum* from Galápagos, a species with characteristics typical of plants growing under extreme environmental conditions.]

———. 1952*a*. Notes on Malvaceae II. Leafl. W. Bot. 6(9): 165–172. [Discusses 5 Galápagos species.]

———. 1952*b*. Notes on Malvaceae III. *Abutilon* and *Pseudabutilon* in the Galápagos Islands. Madroño 11(8): 285–289. [Refers all Galápagos specimens to *A. umbellatum*; makes one new combination, *Pseudabutilon depauperatum*, a species regarded as a link between the 2 genera.]

Kilburn, P. D. 1969. Plants of the Galápagos. Isis 60(3): 386–388. 1 fig. [Discusses Darwin's collections and compares them to more recent ones; Darwin's conclusions in general are still valid, except that he overrated single island endemism.]

Killip, E. P. 1939. Flowering plants collected on the Presidential Cruise of 1938. Smithsonian Misc. Collect. 98(8): 1–4. [Discusses a collection including 20 species, in 12 families, from the Galápagos; notes several new records.]

Koyama, T. 1970. New combinations in the Cyperaceae of the Galápagos Islands. Madroño 20(5): 253–254. [Describes two combinations in *Cyperus* and one in *Rhynchospora*.]

KROEBER, A. L. 1916. Floral relations among the Galápagos Islands. Univ. Calif. Publ. Bot. 6(9): 199–220. [Analyzes the relations of species on various islands, considering such factors as species abundance and geographical position; data presented in 7 tables.]

LARUELLE, J. 1967. Galápagos. Natuurw. Tijdschr. 47: 1–236. 30 pl. 22 figs. [In Dutch, with French resumé. General work including a discussion of flora and vegetation zones, which are subdivided on the basis of soil types.]

LÉVÊQUE, M. R. 1968. Observations sur l'histoire naturelle des Galápagos. Trav. Soc. Bot. Genève 9: 5–7. [In French. General discussion of flora, endemism, and variations from island to island.]

LINSLEY, E. G., C. M. RICK & S. G. STEPHENS. 1966. Observations on the floral relationships of the Galápagos carpenter bee (Hymenoptera: Apidae). Pan-Pacific Entomol. 42: 1–18. [Includes a list of 57 plants in 29 families with distributional data for several islands.]

LLOYD, B. 1964. A pre-Darwinian naturalist in the Galápagos. Not. Galápagos 4: 2–3. [Discusses the visit of Scouler in 1825 and the plants, now in Glasgow herbarium, collected by him.]

LUNDH, J. P. 1966. Notes on *Opuntia* at Puerto Villamil, Galápagos Islands. Cact. Succ. Jour. (Los Angeles) 38: 93–94. [Discusses variations in habit and morphology of *O. echios* var. *inermis*.]

———. 1970. A new variety of *Opuntia megasperma* from the Galápagos Islands. Madroño 20(5): 254. [Describes a variety found only on the west end of San Cristobal.]

MARSHALL, W. T. 1934. Letter. Cact. Succ. Jour. (Los Angeles) 5: 585. [Notes that name of *Cereus* used by Howell [1934*c*] does not agree with treatment in Britton and Rose.]

MOLDENKE, H. N. 1968*a*. Additional notes on the genus *Avicennia*. IV. Phytologia 15(7): 470–477. [Description of *A. germinans* as it appears in the Galápagos.]

———. 1968*b*. The Vervains collected on the Galápagos Islands by Charles Darwin during the voyage of the "Beagle." Phytologia 16(4): 340–342. [Applies new names to 2 Darwinian specimens and mentions 5 other species of *Verbena* known from the islands.]

ONO, M. 1967*a*. The systematic position of *Scalesia* from the viewpoint of chromosome number. Not. Galápagos 9/10: 16–17. [Seeds of 2 species germinated and chromosomes counted: $2n = 68$; concludes genus may be a tetraploid.]

———. 1967*b*. Chromosome number of *Scalesia* (Compositae), an endemic genus of the Galápagos Islands. Jour. Jap. Bot. 42(12): 353–360. 5 figs. [Chromosome number reported (see above); reviews history of genus and its possible affinities.]

ORR, R. T. 1965. Barrington Island. Pacific Disc. 18(5): 23–27. [Popular account, including some discussion of vegetation of the island as well as an offshore islet.]

PORTER, D. M. 1969*a*. *Psidium* (Myrtaceae) in the Galápagos Islands. Ann. Missouri Bot. Gard. 55: 368–371. [Describes one new variety, discusses relationships of endemic species; key provided.]

———. 1969*b*. The flora of the Galápagos Islands. Ann. Missouri Bot. Gard. 55: 173–175. [Describes new flora project, mentioning previous work.]

———. 1969*c*. The genus *Dodonaea* (Sapindaceae) in the Galápagos Islands. Occas. Pap. Calif. Acad. Sci. 81: 1–4. [Discusses two varieties of *D. viscosa*, one pantropical and one endemic.]

———. 1971*a*. Floral gland morphology in *Tribulus* (Zygophyllaceae). Amer. Jour. Bot. 58(5, pt. 2): 466. Abstract. [Morphology of glands in Galápagos *Tribulus* is not species-specific; this may be due to interspecific hybridization.]

———. 1971*b*. Notes on the floral glands in *Tribulus* (Zygophyllaceae). Ann. Missouri Bot. Gard. 58(1): 1–5. 3 figs. [Discusses lack of species differences in intrastaminial glands in Galápagos species; offers evidence that hybridization between the 2 species could have occurred.]

———. 1971*c*. Buttressing in a tropical xerophyte. Biotropica 3(2): 142–144. 1 fig. [Discusses significance of buttress formation by *Bursera graveolens* in the Galápagos.]

REEDER, J. R. & C. G. REEDER. 1970. A new combination in *Trichoneura* from the Galápagos Islands. Madroño 20(5): 253. [Describes a new variety.]

RENDLE, A. B. 1903. The flora of the Galápagos Islands. New Phytol. 2: 135–138. [Review of Robinson (1902); summarizes floral composition, vegetation zones, dispersal of plants and origin of islands, concluding that botanical evidence is opposed to subsidence theory.]

RICK, C. M. 1956. Genetic and systematic studies on accessions of *Lycopersicon* from the Galápagos Islands. Amer. Jour. Bot. 43: 687–696. 15 figs. [Experiments with 2 species show genetic uniformity in first and second generations and a high level of self-pollination.]

———. 1958. The role of natural hybridization in the derivation of cultivated tomatoes of western South America. Econ. Bot. 12: 346–367. 7 figs. [Shows evidence for hybridization between 2 Galápagos species of *Lycopersicon*.]

———. 1963. Biosystematic studies on Galápagos tomatoes. Occas. Pap. Calif. Acad. Sci. 44: 59–77. 7 figs. [Describes 3 types of tomatoes, their population structure, distribution, seed dormancy, compatibility tests and origin; concludes that all 3 belong to a single species, *Lycopersicon esculentum*.]

———. 1966. Some plant-animal relations on the Galápagos Islands. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 215–224. 3 figs. [Pollination relations of 17 species listed in table; notes lack of pollinating insects and high percentage of self-pollination.]

———. 1967. Fruit and pedicel characters derived from Galápagos tomatoes. Econ. Bot. 21(2): 171–184. 12 figs. [Breeding procedures have transferred 7 modifications of fruit and pedicel, some of which may have horticultural value, from Galápagos tomatoes to cultivars with larger fruits.]

——— & R. I. Bowman. 1961. Galápagos tomatoes and tortoises. Evolution 15: 407–417. [Digestion of tomato seeds by native tortoises improves germination; suggests that tortoises are a dispersal agent for tomatoes.]

Riley, L. A. M. 1925. Critical notes on Galápagos plants ("St. George" Pacific Expedition, 1924). Kew Bull. 1925(5): 216–231. [Discusses a collection of 53 species in 25 families; describes 4 new species and 2 new varieties.]

Robinson, B. L. 1902. Flora of the Galápagos Islands. Proc. Amer. Acad. Arts 38(4): 77–269. 3 pl. [Discusses composition and affinities of flora, lists 86 species of monocots, one new, and 383 species of dicots, 19 of which are new; distribution data summarized in tables.]

——— & J. M. Greenman. 1895. On the flora of the Galápagos Islands, as shown by the collections of Dr. G. Baur. Amer. Jour. Sci., Ser. 3. 50: 135–149. [Lists a collection of 38 monocots and 158 dicots, 17 of which are new or noteworthy; discusses variation of plants on different islands; distribution data presented in table.]

Rose, J. N. 1892. List of plants collected by the U. S. S. *Albatross* in 1887–97 along the western coast of America. 2. List of plants from the Galápagos Islands. Contr. U. S. Natl. Herb. 1: 136–138. [Briefly reviews other collections and lists 6 species of monocots and 24 species of dicots.]

St.-John, H. 1937. A new *Calandrinia* from the Galápagos Islands. Amer. Jour. Bot. 24: 95. [Describes *C. galapagosa* from San Cristobal, a plant identified by Stewart as *Portulaca lutea*.]

Schofield, E. K. 1970. Field guide to some common Galápagos plants. Ohio State Univ. Research Foundation. 42 pp. 19 pl. [Line drawings accompanied by short non-technical captions designed to help visitors to the islands recognize the more common plants.]

———. 1971. A field guide to some common Galápagos plants. Lindblad Travel, Inc., New York. [Shorter version of guide to be distributed to tourists visiting the islands.]

Setchell, W. A. 1935. Pacific insular floras and Pacific paleogeography. Amer. Naturalist 69: 289–310. 1 fig. [Reviews work by Hooker and Hemsley on Galápagos flora; discusses migration routes, concluding that woody Compositae migrated from southern to western South America and then to islands.]

Sherff, E. E. 1947. Additions to the genera *Scalesia* Arn. and *Hidalgoa* Llave and Lex. (family Compositae). Publ. Field Mus. Nat. Hist., Bot. Ser. 23(7): 333–336. [Makes a new combination, *S. menziesii*; collected in 1795 on the Vancouver voyage, in Hawaii.]

———. 1949. Miscellaneous notes on dicotyledonous plants. Amer. Jour. Bot. 36: 499–511. 2 figs. [Discusses *S. menziesii* (above) and concludes that specimen probably was collected in Galápagos.]

Stebbins, G. L. 1966. Variation and adaptation in Galápagos plants. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press, Berkeley and Los Angeles. Pp. 46–54. [Reviews history of botanical collections, discusses origin of flora, affinities, and evolutionary patterns; suggests groups that need further study.]

Stephens, S. G. 1958. Salt water tolerance of seeds of *Gossypium* species as a possible factor in seed dispersal. Amer. Naturalist 92: 83–92. [Seeds of Galápagos species have ability to float and are tolerant to salt water; dispersal by water or by man could account for species on islands.]

——— & C. M. Rick. 1966. Problems on the origin, dispersal, and establishment of the Galápagos cottons. *In* R. I. Bowman (editor), "The Galápagos." Univ. Calif. Press,

Berkeley and Los Angeles. Pp. 201–208. 3 figs. [Discusses the 2 Galápagos species of *Gossypium*, their possible origin and affinities; chromosome numbers given.]

STEWART, A. 1911. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906. II. A botanical survey of the Galápagos Islands. Proc. Calif. Acad. Sci., Ser. 4. 1: 7–288. 19 pl. [Catalogue of plants, including 11 families of monocots and 66 families of dicots; table summarizes distribution of all species; discusses vegetation zones, ecological factors influencing plants, origin of Galápagos and relationships of flora.]

———. 1915*a*. Notes on the forms of *Castela galapageia*. Amer. Jour. Bot. 2: 279–288. 10 figs. [Describes 5 forms and shows variations in leaf shape.]

———. 1915*b*. Some observations concerning the botanical conditions on the Galápagos Islands. Trans. Wisconsin Acad. Sci. 18: 272–340. [Gives detailed description of vegetation of nearly every island.]

———. 1915*c*. Further observation on the origin of the Galápagos Islands. Pl. World 18: 192–200. [Reviews his floristic studies which indicate the islands are oceanic but may have once been connected to each other; flora originated by long-distance dispersal.]

SVENSON, H. K. 1930*a*. Report on a botanical exploration trip to the Galápagos Islands. Brooklyn Bot. Gard. Rec. 19(6): 269–284. 13 figs. [Describes vegetation of Santa Cruz, Floreana and Genovesa.]

———. 1930*b*. The vegetation of Indefatigable Island. Bull. New York Zool. Soc. 33(4): 163–170. 13 figs. [Describes vegetation from shore to 2000 feet, including *Miconia* zone, as seen on first ascent to summit of island.

———. 1935. Plants of the Astor Expedition, 1930 (Galápagos and Cocos Islands). Amer. Jour. Bot. 22: 208–277. 7 pl. [Discusses flora of Santa Cruz, with a table showing altitudinal distribution of plants, and a collection including 50 families of flowering plants.]

———. 1939. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 37. The Cyperaceae. Proc. Calif. Acad. Sci., Ser. 4. 22(8): 187–193. [Lists 30 species, giving distribution of 13 and including 6 new records; discusses ecological tolerances of some species on Santa Cruz.]

———. 1942*a*. Origin of plants on the Galápagos Islands. Proc. 8th Amer. Sci. Congr. 3: 285–286. [Notes relationship to flora of South America and discusses means of dispersal to islands.]

———. 1942*b*. Relation of the Galápagos flora to that of the mainland. Amer. Jour. Bot., Suppl. 29(10): 185. Abstract. [Notes similarity of climate in Ecuador and relationship of floras.]

———. 1945. A brief review of the Galápagos flora. *In* F. Verdoorn (editor), "Plants and Plant Science in Latin America." Chronica Botanica, Waltham, Mass. Pp. 149–150. [Reviews history, climate, general aspects of flora and gives short summary of vegetation zones.]

———. 1946*a*. Vegetation of the coast of Ecuador and Peru and its relation to the Galápagos Islands. I. Geographical relations of the flora. Amer. Jour. Bot. 33(5): 394–426. 20 figs. [Discusses exploration, geology, climate, vegetation zones and provides distribution maps for 23 plants.]

———. 1946*b*. Vegetation of the coast of Ecuador and Peru and its relation to the Galápagos Islands. II. Catalogue of plants. Amer. Jour. Bot. 33(6): 427–498. 22 pl. [Lists plants in 65 families, including 93 Galápagos species.]

———. 1957. Vegetation provinces of the Pacific-Galápagean. The Galápagos Islands. Proc. 8th Pacific Sci. Congr. 4: 162–166. [Discusses adaptive radiation of plants in coastal areas and succession on new lava flows.]

———. 1963. Opportunities for botanical study on the Galápagos Islands. Occas. Pap. Calif. Acad. Sci. 44: 53–58. [Discusses problems such as seed germination, variation within species, distribution in relation to climate and adaptive radiation.]

SZYMKIEWICZ, D. 1938. Quatrième contribution statistique à la géographie floristique. Acta Soc. Bot. Poloniae 15(1): 15–22. 3 figs. [In French. Discusses variations in flora among islands, concludes Floreana is oldest island and Fernandina youngest; table lists number of species and endemics on each island.]

TAYLOR, T. W. J. 1940. Plant pigments in the Galápagos Islands. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 129(855): 230–237. [Describes method of identifying anthocyanins in the field; table lists distribution of pigments in 36 flowering plants and one fern.]

THORNTON, I. 1971. Darwin's Islands. A Natural History of the Galápagos. Natural History Press, Garden City, N.Y. 322 pp. 28 figs. 36 pl. [General discussion including origin,

dispersal and evolution of flora; distribution maps for several plants, *e. g. Scalesia* and *Alternanthera*, provided.]

VARIGNY, M. H. DE. 1892. Un voyage scientifique aux Îles Galápagos. Rev. Sci., Ser. 3. 24: 391–400. [In French. Mentions plants of several islands, including cacti on Española and Santa Fé.]

WALKINGTON, D. L. & E. F. ANDERSON. 1967. A study of some neotropical opuntias. II. Morphology and chemistry. Amer. Jour. Bot. 54(5, pt. 2): 645–646. Abstract. [Measurements of vegetative and reproductive structures and chromatograms of stem extracts show that Galápagos opuntias fall into 2 groups. (*cf.* Dawson, 1965).]

WATERFALL, U. T. 1968. A new species of *Physalis* from the Galápagos Islands. Rhodora 70(783): 408–409. [Describes *P. galapagoënsis* and compares it to other species; chromosome count, $n = 12$.]

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THE SYSTEMATICS OF LOPEZIEAE (ONAGRACEAE)[1]

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Members of the genus *Lopezia* (Onagraceae) have long fascinated students of floral biology because of their flowers, which are both intricate and reduced in the number of their parts. In his review of the group, Munz (1961: 73) pointed out that further studies would be necessary even to set reasonable generic limits in Lopezieae, much less specific ones. The present revision represents several years of study in the field, experimental greenhouse, and herbarium, and brings to bear rather extensive information from morphology, floral anatomy (Eyde & Morgan, 1973), cytology (Plitmann, Raven & Tai, 1974), pollination biology (Raven, Breedlove, Gregory & Plitmann, 1974) on the classification of the group.

As Eyde and Morgan (1973) have emphasized, this small group of 21 species is of unusual interest in its mixture of generalized and derivative floral features. Largely restricted to Mexico, with three species extending to Guatemala and one to El Salvador and one subspecies confined to El Salvador, Costa Rica, and Panama, *Lopezia* occupies a wide variety of habitats. Some species are regularly visited and pollinated by hummingbirds; other by flies, principally syrphids; and still others are autogamous. Also of interest is the range of chromosome numbers in the group, which includes not only $n = 11$, presumbably basic for the family as a

[1] We are most grateful for the support provided through a series of grants from the U. S. National Science Foundation to Raven; to the National Institutes of Health–U. S. Public Health Service for a training grant in population biology in the Department of Biological Sciences at Stanford University, which made possible the first year of Plitmann's studies at Stanford University; and to those in charge of the Department of Biological Sciences at Stanford University and the Department of Plant Biology of the Carnegie Institution of Washington, Stanford, California, for the provision of facilities that made our experimental studies of *Lopezia* possible. We have profited greatly from our collaboration with Richard H. Eyde, who has carried out a detailed study of floral structure and evolution in the genus (Eyde & Morgan, 1973) and has kindly reviewed the present manuscript, offering many helpful suggestions. Julia Spranza drew the illustrations, and Saichi Kawahara made the maps.

We are also indebted to those in charge of the herbaria of the following institutions, who made material available for our study: Arnold Arboretum (A); L. H. Bailey Hortorium, Cornell University (BH); British Museum (Natural History) (BM); Museo Nacional, San José, Costa Rica (CR); Dudley Herbarium, Stanford University (DS); Field Museum of Natural History, Chicago (F); Conservatoire et Jardin botaniques, Genève (G); Gray Herbarium, Harvard University (GH); Botanische Anstalten der Martin Luther Universität, Halle (HAL); Instituto Politécnico Nacional, México (IPN); Royal Botanic Gardens, Kew (K); Botanische Staatssammlung, München (M); Instituto Botánico "Antonio José Cavanilles," Madrid (MA); Herbario Nacional del Instituto de Biología de la Universidad Nacional de México, México, D.F. (MEXU); University of Michigan, Ann Arbor (MICH); Missouri Botanical Garden (MO); The New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); Pomona College, Claremont, Calif. (POM); Rancho Santa Ana Botanic Garden, Claremont, Calif. (RSA); Naturhistoriska Riksmuseum, Stockholm (S); University of Texas, Austin (TEX); University of California, Berkeley (UC); U. S. National Museum, Washington, D.C. (US); Naturhistorisches Museum, Wien (W); Botanischer Garten and Museum der Universität Zürich (Z).

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Ann. Missouri Bot. Gard. 60: 478–563. 1973.

whole, but also $n = 10$, 9, 8, 7, and 22. Similar differences in gametic chromosome number, reflecting aneuploid change, are known in the family Onagraceae otherwise only in the annual genus *Clarkia*. Our studies of interspecific crossability and evolution in the group are still underway, but we hope that the present systematic account will constitute a convenient basis for further research on these fascinating plants.

Introduction

As a result of our studies and those of Eyde and Morgan (1973), we have concluded that relationships within the distinctive tribe Lopezieae Spach (1835) can be expressed best by grouping all species in a single genus, *Lopezia*. Our reasons for proposing this arrangement will be discussed in the present paper, but an outline of the sections and species we have recognized, with the names of the segregate genera to which these species have been referred in the past, is given now as an aid to understanding our introductory discussion.

Lopezia Cav.

I. Sect. *Diplandra* (Hook. & Arn.) Plitmann, Raven & Breedlove
   1. *L. lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove (*Diplandra*)

II. Sect. *Riesenbachia* (Presl) Plitmann, Raven & Breedlove
   2. *L. semeiandra* Plitmann, Raven & Breedlove (*Semeiandra*)
   3. *L. riesenbachia* Plitmann, Raven & Breedlove (*Riesenbachia*)

III. Sect. *Jehlia* (Rose) Plitmann, Raven & Breedlove
   4. *L. longiflora* (Decne.) Plitmann, Raven & Breedlove (*Pseudolopezia*)
   5. *L. grandiflora* Zucc. (*Jehlia*)
   6. *L. langmaniae* Miranda

VI. Sect. *Lopezia*
   7. *L. hintonii* Foster
   8. *L. miniata* Lag. *ex* DC
   9. *L. suffrutescens* Munz
   10. *L. nuevo-leonis* Plitmann, Raven & Breedlove
   11. *L. cornuta* S. Wats.
   12. *L. ciliatula* Plitmann, Raven & Breedlove
   13. *L. trichota* Schlecht.
   14. *L. racemosa* Cav.
   15. *L. conjugens* T. S. Brandegee
   16. *L. smithii* Rose

V. Sect. *Nannolopezia* Plitmann, Raven & Breedlove
   17. *L. gracilis* S. Wats.

VI. Sect. *Pelozia* (Rose) Plitmann, Raven & Breedlove
   18. *L. laciniata* (Rose) M. E. Jones (*Pelozia*)
   19. *L. gentryi* (Munz) Plitmann, Raven & Breedlove
   20. *L. clavata* T. S. Brandegee (*Pelozia*)
   21. *L. sinaloensis* Munz

FIGURES 1–10. Seedlings of *Lopezia*.—1. *L. lopezioides*.—2. *L. riesenbachia*.—3. *L. clavata*.—4. *L. cornuta*.—5. *L. miniata*.—6. *L. racemosa* (*L. hirsuta*).—7. *L. miniata*.—8. *L. racemosa* (*L. coronata*).—9. *L. gentryi*.—10. *L. gracilis*. Grown at Stanford University in winter of 1967–8.

DISCUSSION OF CHARACTERS

Some of the characters which have proved useful, alone or in combination, in assessing relationships among the species of *Lopezia* and in understanding the phylogeny of the genus are discussed in the following pages.

Germination and seedling characteristics.—The germination of all species of *Lopezia* is epigeal. Generally the young cotyledons are suborbicular to ovate; in most cases their petiole elongates, sooner or later, to almost the length of the blade. Mature cotyledons are more or less ovate, subretuse to obtuse at base. The young leaves are usually linear or lanceolate to oblong but become much wider when mature. As a rule, the first leaves are opposite. Marginal teeth are developed even in the first pair of leaves, though the teeth are less distinct in *L. cornuta* and *L. miniata*, for example, than in *L. racemosa* or *L. nuevo-leonis*.

A few species can already be recognized at the seedling stage (Figs. 1–10). Those of *Lopezia lopezioides* have fleshy, thick and rounded juvenile leaves. In *L. racemosa* subsp. *moelchenensis* the early leaves are dark green or red-brown in color and elongate (oblong or elliptic lanceolate). In *L. nuevo-leonis* the first leaves are already rather fleshy, acutely serrate, and borne on angular stems. The seedlings of *L. riesenbachia* and *L. clavata* have remotely serrate cotyledons; the leaves are light green, more or less acutely serrate and relatively thin. The seedlings of *L. gracilis*, *L. gentryi*, and *L. laciniata* have dark green juvenile leaves, narrower than in most species (linear to lanceolate or narrowly ovate)

and ± elongate. In *L. laciniata* subsp. *ovata*, however, the juvenile leaves are relatively wide, and—much like the cotyledons—retuse at the base. All other seedlings are ± similar, although they differ in hue from strain to strain (either dark red or green), in growth rate and hence in length of the hypocotyl, and in pubescence. Sometimes (*e.g.* in *L. cornuta*) the seedlings are long-hairy whereas the mature plants are sparsely or shortly so.

The variability of the seedlings corresponds with that of the mature plant. In the highly variable *Lopezia racemosa* group, for example, they vary in length of the hypocotyl and stem, color, pubescence, size of leaves. Thus seedlings of the more polymorphic groups (*e.g. L. miniata* subsp. *miniata*) show wide variation in contrast to those of the more uniform taxa.

Habit.—Most species of *Lopezia* are herbaceous annuals, while a few are perennial or even shrubby. In certain groups (*L. laciniata–L. gentryi*) the annuals are sharply distinct from the perennials, in others (sect. *Lopezia*) annuals and perennials may occur in the same species and intergrade with one another. The stems are usually ascending or erect; in *L. laciniata* and *L. racemosa* subsp. *moelchenensis* they are prostrate or decumbent, root at the nodes, and could be described as stolons. The stems of some species are virgate (*L. lopezioides*), while they are recurved or drooping in others (*L. longiflora, L. semeiandra* at the summit).

The stems and branches are generally terete, yet in a few species (*L. cornuta, L. trichota, L. nuevo-leonis*) they are angular. In *L. smithii* the stems are somewhat winged. Nearly all bird-pollinated species of *Lopezia* have the stems thickened and fleshy below the ground level; exceptional is *L. semeiandra.* Among the fly-pollinated species *L. trichota* has tuberous roots and passes the dry season in a leafless condition, whereas *L. miniata* subsp. *paniculata* has somewhat bulbous ones.

Fasciation has been rather commonly observed in *Lopezia*, particularly in *L. racemosa*, as in many other Onagraceae (*e.g. Clarkia unguiculata* Lindl., *Epilobium angustifolium* L., *Oenothera drummondii* Hook.; see De Vries, 1894, 1899; Knox, 1907, 1908; Johansen, 1930). Fasciation leads to the development of abortive, green flowers (virescence and frondescence, as observed for example in *Oenothera* by Gates, 1910). Fasciation is more abundant in certain populations, such as the hirsute plants of *L. racemosa* subsp. *racemosa* from Mt. Orizaba and its environs (Veracruz). This suggests that certain strains are more susceptible to factors, such as infection by nematodes, which promote this condition.

Leaves.—These are highly variable in shape (oblong-linear to broadly ovate, ± serrate) and size. Several species, however, are characterized by some outstanding traits of the leaves. Though the leaves are generally alternate, they are ± opposite in *Lopezia lopezioides, L. conjugens*, and *L. riesenbachia.* They are thin in *L. clavata*, somewhat thick or fleshy in *L. nuevo-leonis* and *L. racemosa* subsp. *moelchenensis*; relatively narrow in the latter as well as in *L. laciniata* subsp. *laciniata* and *L. gentryi*; narrow and short in *L. gracilis*; infrequently (*L. racemosa* subsp. *moelchenensis, L. smithii, L. gracilis* and *L. lopezioides*) they

are short-petioled. They are acutely serrate in *L. nuevo-leonis*, *L. suffrutescens* and *L. clavata*, and shallowly so and even subentire in *L. conjugens*, *L. gracilis*, *L. cornuta*, and *L. sinaloensis*. The teeth are glandulose in *L. longiflora* and colored with "oil cells" in *L. racemosa* subsp. *moelchenensis*. *Lopezia smithii* is distinctive in its unique leaf-base; an unequal base is found also in *L. longiflora*, *L. ciliatula* and *L. trichota*. The petioles are rarely winged (*L. conjugens*, *L. riesenbachia*, *L. clavata*, *L. sinaloensis*, *L. ciliatula*).

The veins of the leaves are quite variable in number; the extremes are *Lopezia trichota*, *L. gracilis* and *L. laciniata* with indistinct or very few veins, as distinct from *L. langmaniae* and *L. semeiandra* with their large, many-veined (to 27 on each side) leaves.

Stipules are present in all species, but tiny, rudimentary and caducous. They sometimes persist longer, especially on the vigorous growth of shrubby species.

Pubescence.—The vegetative parts of most species of the tribe are pubescent, with hairs usually ± appressed, varying in length, usually pale in shade but infrequently colored. Spreading hairs are present in *Lopezia lopezioides* and *L. sinaloensis* (retrorse), and sometimes in *L. miniata*, especially on the stem. They are somewhat incurved in *L. ciliatula*, silky in *L. langmaniae* and to some extent in *L. semeiandra*, mixed with glandular ones in *L. riesenbachia*, *L. semeiandra* and on the inflorescence and sepals of *L. lopezioides*. Six taxa are glabrous or nearly so: *L. gracilis*, *L. suffrutescens*, *L. nuevo-leonis* (but pedicels hairy on one side), *L. racemosa* subsp. *moelchenensis*, *L. trichota* and *L. gentryi*. Stems, leaves, pedicels and sepals are most commonly pubescent (the latter two always have shorter hairs). There are, however, special cases in which other parts are hairy as well: ciliate petals are found in *L. ciliatula*, *L. trichota*, *L. longiflora* (the lower sometimes ± ciliate) and *L. racemosa* (claws only); the style is hairy in *L. trichota*, *L. grandiflora* (sometimes pilose) and *L. semeiandra*; the capsules are pubescent in *L. langmaniae* (slightly hairy-tubercled), *L. ciliatula* (strigulose), *L. riesenbachia* (hirtellous-puberulent), *L. laciniata* (± puberulent), *L. gentryi* (setaceous with tubercled hairs) and *L. semeiandra* (± puberulent-hirtellous). In addition, *L. smithii* uniquely has upper petals with clavate hairs around the glands, and *L. semeiandra* has a floral tube which is hirsute on both sides and stamens and petals which are ± hairy outside at the base. Within some species, such as the polymorphic *L. miniata* and *L. racemosa*, the hairs may vary in length and density; they may be of various colors (usually whitish but sometimes rusty to even purplish), straight or recurved, appressed to patent, and sometimes all or partly glandulose throughout the plant or on particular organs. The pubescence is variable almost independently on the different parts of the plant (pedicels, calyx, style, ovary and capsule).

Inflorescence.—In most species of the tribe the inflorescence is branched, leafy, and racemose. The racemes are usually dense, even corymbiform, at the apex, and more loose and leafy below, with small bract-like leaves. There are, however, some outstanding modifications: The inflorescence is characteristically paniculate and crowded in *Lopezia miniata* subsp. *paniculata* and corymbose in

L. suffrutescens and rarely in *L. racemosa*. In a few species it is typically few-branched or simple (*L. cornuta*), few-flowered (*L. sinaloensis*), distinctly leafy throughout with upper leaves less reduced (*L. racemosa* subsp. *moelchenensis*) or especially slender (*L. hintonii*, *L. conjugens*, *L. gracilis*). In some species, a wide variation is displayed in length of racemes (which, besides, are elongated toward fruiting) and the amount of branching (simple or short racemes to paniculate or large inflorescence), and even more in the number of flowers, capsules and seeds (in a single population or on an individual plant).

Pedicels.—The pedicels, more so than the whole inflorescence, are quite uniform in shape and inclination. Exceptional are *Lopezia ciliatula* with its ± winged pedicels, and *L. cornuta* with its typically drooping ones in fruit. They are sometimes drooping or antrorse in *L. racemosa* and sigmoid-spreading in fruits of *L. sinaloensis*. Relatively long pedicels (longer than 3 cm) occur in *L. laciniata* and sometimes in *L. racemosa* subsp. *moelchenensis*.

Flowers and pollination systems.—The flowers of the species of *Lopezia* fall into two broadly defined groups, according to the mode of pollination. In the five bird-pollinated species—*L. grandiflora*, *L. langmaniae*, *L. longiflora*, *L. lopezioides*, and *L. semeiandra*—the flowers are red; ± tubular in shape, with the sepals and petals directed forward; and produce abundant nectar from the prominent interstaminal nectaries at the base of the tube. We have actually observed visits by hummingbirds in the field in all of these species (Raven, Breedlove, Gregory & Plitmann, 1974). In the remaining species of the genus, with the possible exception of the poorly known *L. hintonii*, the flowers are lavender, rose-purple, magenta, purplish, or white; the sepals and petals spread widely from the top of the constricted "neck" at the summit of the ovary; and smaller amounts of nectar are produced. The flowers of these species are visited by and usually pollinated by flies, especially Syrphidae, or are autogamous. We have observed fly-pollination, with occasional visits by bees and other insects, in *Lopezia cornuta*, *L. laciniata* subsp. *ovata*, *L. miniata*, *L. racemosa*, and *L. trichota* (Raven, Breedlove, Gregory & Plitmann, 1974). Our field observations indicate that *L. ciliatula*, *L. gentryi*, *L. gracilis*, and *L. riesenbachia* are rarely visited by insects and largely autogamous; and *L. clavata* and *L. nuevo-leonis* are highly autogamous when grown in the experimental greenhouse, but perhaps partly outcrossing in the field. *Lopezia suffrutescens*, which we have observed only briefly in the field but have grown in the experimental greenhouse, is almost exclusively outcrossed and evidently fly-pollinated, as is *L. miniata* subsp. *paniculata*, which we have grown in the experimental greenhouse but not seen in the field. We have not observed living plants of *L. hintonii*, *L. sinaloensis*, *L. conjugens*, or *L. smithii*, but judge that the first is definitely an outcrossing species.

The flowers of the bird-pollinated species range from 1.1–8 cm in length, those of the others having petals to 1 cm long. In one of the bird-pollinated species, *L. semeiandra*, there is a definite floral tube formed by the union of the floral parts above the ovary. The proximal part of this tube is divided by a median septum into two deep pockets lined with nectariferous tissue. The column

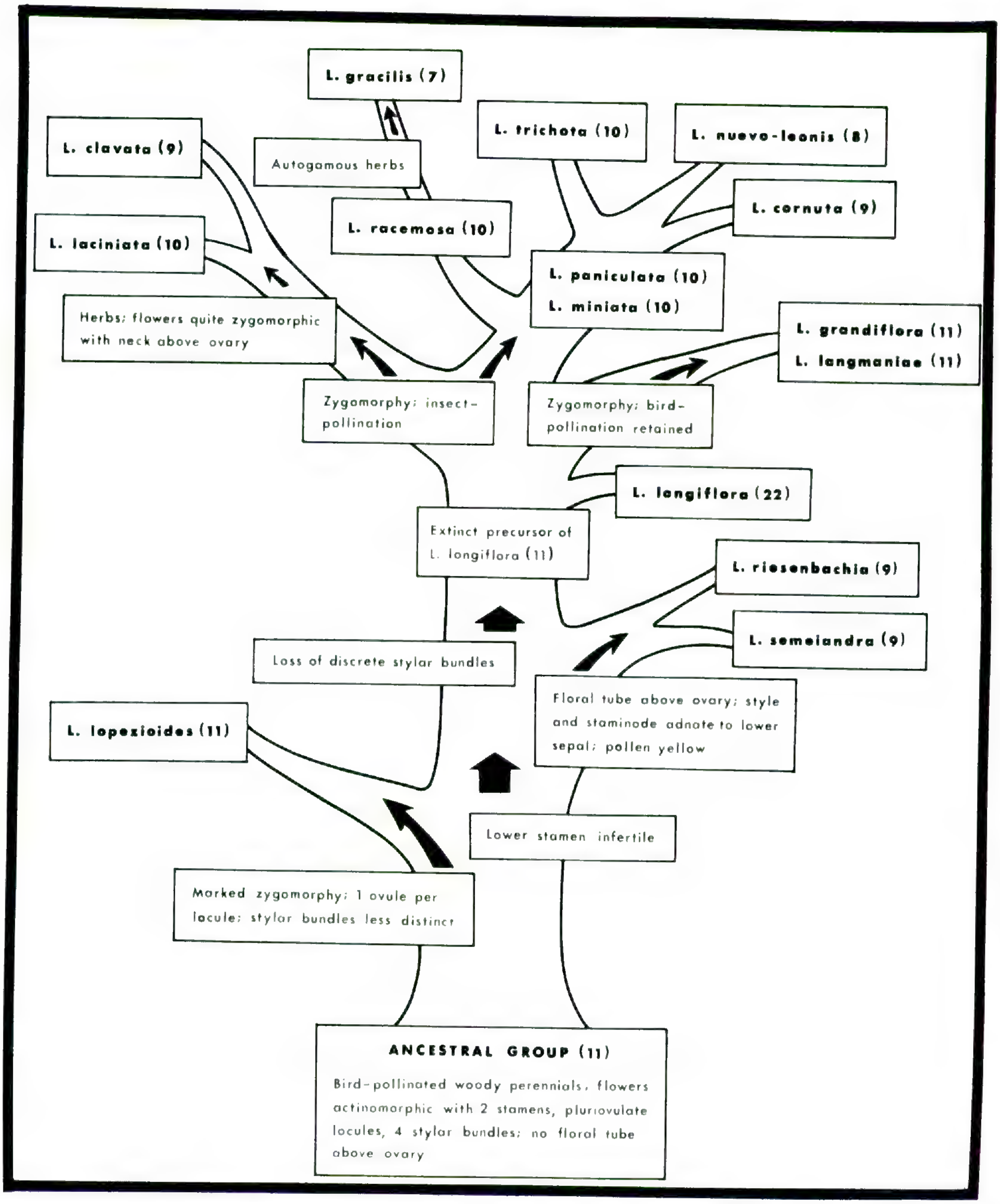


FIGURE 11. Phylogeny of *Lopezia*, as postulated by Eyde and Morgan (1973). We would now consider it more likely that *L. gracilis* arose below the base of the branch leading to *L. racemosa*, as explained in the text. *Lopezia paniculata* is considered a subspecies of *L. miniata*, following a review of data not available at the time the paper of Eyde and Morgan (1973) went to press. Gametic chromosome numbers indicated in parentheses. Figure reprinted by permission of the authors and the *American Journal of Botany*.

including the style and stamens is adnate to the lower side of the floral tube. These features are found only in this species and in the autogamous *L. riesenbachia*, indicating their common origin as an early and independent evolutionary line within the group (Eyde & Morgan, 1973). In fly-pollinated species of sect.

Pelozia, an advanced group marked by extreme floral zygomorphy, the constriction above the ovary is prolonged into a neck, and all floral parts except the staminode and lower sepal are greatly displaced to the upper side of the flower and united to varying degrees (Fig. 11). All species have sternotribic pollination.

Aestivation.—Aestivation in *Lopezia* is generally imbricate; it is imbricate to almost convolute in species in which the upper petals are relatively wide (*L. lopeziodes*, *L. grandiflora*). More commonly the upper petals are partly overlapped by the lower. Exceptional with valvate imbrication are *L. langmaniae*, with its rudimentary petals, and *L. semeiandra*, with its greatly reduced linear ones. The "resupinate" arrangement of petals in *L. laciniata* and *L. gentryi* is already pronounced in bud, in which the lower (outer) petals, partly overlapping the upper ones, are distinctly smaller.

Petals.—The petals, variable as they are, present good diagnostic criteria. They may be wide (*L. lopezioides*, *L. grandiflora*) or long (*L. longiflora*, *L. semeiandra*), small (*L. ciliatula*, *L. gracilis*, *L. gentryi*) or evidently reduced (*L. langmaniae*). Usually the lower ones are larger, but it is the other way around in *L. trichota* and especially in sect. *Pelozia*, whereas subequal ones characterize the bird-pollinated species. The petals are ± similar in outline, the lower ones oblong-obovate, the upper oblong-linear to oblanceolate. Nevertheless, there are some marked distinctions. For example, all petals are somewhat spatulate in *L. suffrutescens*, linear-oblanceolate in *L. longiflora* and narrowly linear in *L. semeiandra*; the upper ones are narrowly linear-spatulate in *L. ciliatula*, the lower ones are obovate-suborbicular in *L. gracilis*. The apices may be entire (*L. racemosa*), or sinuate-crenulate to suberose-denticulate (*L. grandiflora*, *L. hintonii*, *L. miniata*), or laciniate (*L. laciniata*, *L. gentryi*). In other morphological features of the petals, *Lopezia* can be divided into four groups: Petals (at least the upper) sessile and not auricled (*L. longiflora*, *L. semeiandra*); sessile but auricled (*L. suffrutescens*, *L. ciliatula*); auricled and more or less clawed or attenuate (*L. hintonii* with winged claws and obsolete auricles at upper petals; *L. suffrutescens*, *L. miniata*, *L. nuevo-leonis*); not auricled or hardly so and clawed (with limb truncate or cuneate) or attenuate (all the rest).

Glands and nectaries.—Massive interstaminal nectaries characterize the bird-pollinated species of *Lopezia* (Eyde & Morgan, 1973); these species produce abundant nectar. In other species, which produce limited amounts of nectar, or perhaps in some cases none at all, interstaminal nectaries are also present, and very well developed in some (*e.g. L. racemosa*; Eyde & Morgan, 1973). In addition, most species of the genus have shiny, conspicuous glands, or pseudonectaries, on the upper petals. In the fly-pollinated and autogamous species of sect. *Lopezia* and sect. *Nannolopezia* there are either one or two on each upper petal, except in *L. conjugens* (sect. *Lopezia*). In sect. *Pelozia*, in which the upper petals and sepals are united, the upper sepal has a prominent tubercle of this nature at the level at which the upper sepals and petals diverge from it. This tubercle, which cannot be homologous with the glands on the upper petals

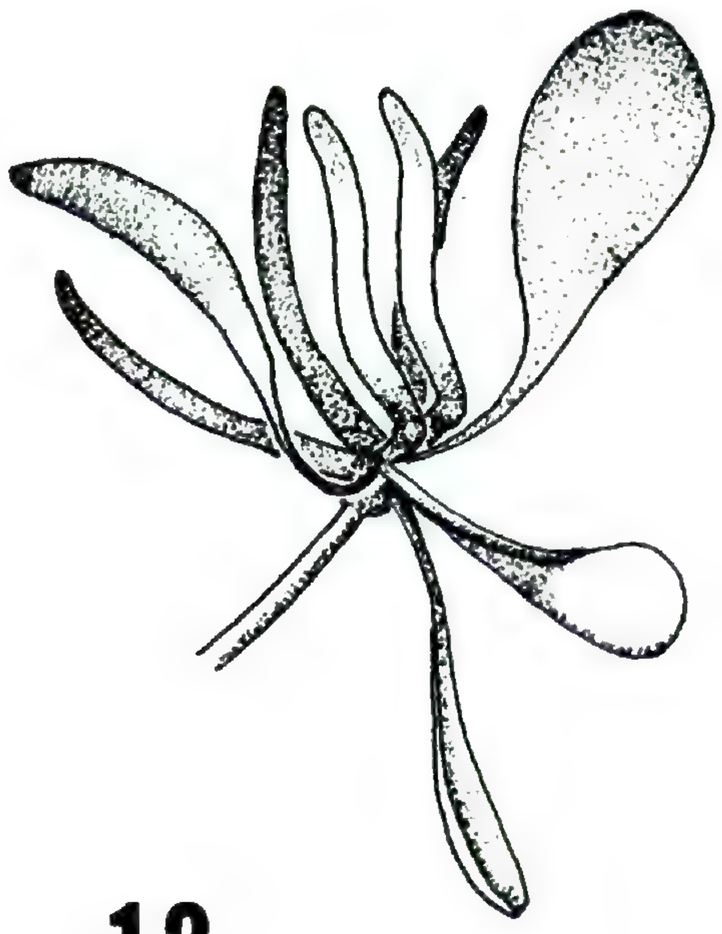
of the three sections just mentioned, is flanked by weakly developed glandlike dots on the upper petals; they might be homologous with the pseudonectaries in other species. Eyde and Morgan (1973) have hypothesized, on the basis of densely staining areas they observed in the upper petals of *L. cornuta* and *L. gracilis*, that a volatile chemical attractant may supplement the visual cues in the fly-pollinated species of *Lopezia*.

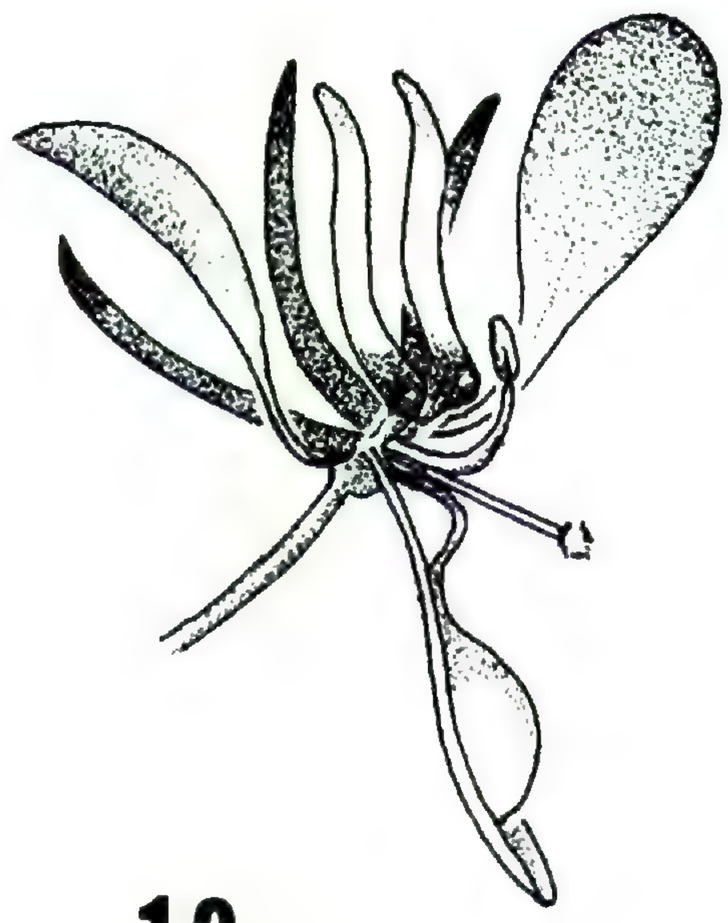
Among the bird-pollinated species of *Lopezia*, there are no comparable glands, although the upper petals of *L. grandiflora* and *L. langmaniae* do have swollen areas on the upper petals, which may be homologous with and the precursors, in an evolutionary sense, of the glands on the upper petals of the insect-pollinated species (Eyde & Morgan, 1973). *Lopezia riesenbachia*, an autogamous species with obsolete interstaminal nectaries that is very closely related to the bird-pollinated *L. semeiandra*, usually has a tiny, arcuate or dot-like tubercle near the base of each upper petal; its significance is obscure, but it might be analogous with the somewhat similar structure found in *L. langmaniae*. Finally, in *L. conjugens*, clearly a member of sect. *Lopezia* and not otherwise remarkably different from other species of the section, the glands have evidently been lost.

Slight variations in the size, shape, and exact position of the glands on the upper petals and upper sepal have been greatly exaggerated in importance by some taxonomists (*e.g.* Rose, 1909; Sprague & Riley, 1924), and this has been one of the factors which has led to a proliferation of specific names in the group. Fifty years ago nearly three times as many species were recognized as are accepted in the present revision.

Pollen.—The pollen of most species is blue, that of *Lopezia clavata, L. sinaloensis, L. semeiandra*, and *L. riesenbachia* yellow. As suggested by Eyde and Morgan (1973), yellow pollen must have originated independently in the common ancestor of the first two species and in the common ancestor of the last two. The anther is yellowish in species with yellow pollen, bluish in most of the rest; in *L. suffrutescens, L. laciniata* and *L. gentryi* it is red. Four-porate pollen grains are frequent in place of the normally three-porate ones in polyploid ($n = 20$) individuals of *L. racemosa* (both subspecies).

The snapping phenomenon.—In all species of *Lopezia* except *L. lopezioides*, the lower stamen is sterile. This flattened or spoon-shaped staminode characteristically enfolds the anther of the fertile stamen in bud (Fig. 12). Although the dehiscence of this anther is fundamentally introrse, it rotates through 180° by a twisting of the terminal, slender portion of the filament just before the flower opens, presumably owing to the spatial relationships in the bud coupled with differential growth patterns. After the flower opens, the mature stamen, shedding pollen, is usually deflected downward, below the main axis of the flower; after it sheds its pollen, which is bound together in a mass by the viscine threads characteristic of the pollen of Onagraceae, it is deflected still farther downward, and the style grows outward to a position in which the tardily maturing stigma occupies the same spatial relationship with the rest of the flower





FIGURES 12–13. Flowers of *Lopezia racemosa*, 5.—12. Before snapping of fertile stamen upward; it is held in place and under tension by enfolding staminode.—13. After fertile stamen has snapped upward and staminode moved downward; the style has grown outward and the stigma occupies essentially the position of the fertile anther in Fig. 12.

that the shedding anther did previously (Fig. 13). Outcrossing species of *Lopezia* are thus strongly protandrous, and a pollinator moving from flower to flower has a high probability of effecting cross-pollination.

This general outline of floral biology holds for the bird-pollinated species of *Lopezia* (*L. semeiandra*, *L. longiflora*, *L. grandiflora*, *L. langmaniae*). In all species of sect. *Lopezia*[5] the rotated fertile anther is held under tension by the enfolding staminode and snaps the pollen up onto the venter of any fly that alights and orients itself toward the pseudonectaries. This interesting phenomenon has been observed and discussed by many students for nearly 200 years (reviews in Raven *et al.*, 1974; Eyde & Morgan, 1973). The snapping phenomenon is not found in the four species of sect. *Pelozia*, nor in the autogamous *L. gracilis* (sect. *Nannolopezia*).

Because of the distribution of the snapping phenomenon among the species of *Lopezia*, we hypothesize that it evolved in the common ancestor of sect. *Lopezia*, and that the evolution of the mechanism was a single, unique event. This implies that sect. *Pelozia* was derived from its common ancestor with sect. *Lopezia* before the evolution of the snapping mechanism. It also lends support to the notion that *Lopezia gracilis*, the only species of sect. *Nannolopezia*, was not derived from sect. *Lopezia*, contrary to Fig. 11.

Morphological variation in the staminode is fairly extensive and useful in some instances in evaluating the degree of similarity between taxa. It is variable in length, proportion, and outline, as well as in color. In *Lopezia laciniata* and *L. gentryi*, not characterized by the snapping mechanism, it is linear and concave;

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[5] Unfortunately, we have not been able to examine one of the most critical species assigned to this group, *L. hintonii*, in a living condition.

in the autogamous *L. riesenbachia* and *L. clavata*, it is broad and indistinctly clawed; and in most fly-pollinated species, it is somewhat spoon-shaped and very distinctly clawed, the blade enfolding the fertile stamen and holding it under tension at maturity. A reduced uniloculate anther has been observed very rarely on the staminode in *L. grandiflora* and in *L. langmaniae*.

Capsules.—The main morphological characters of the capsule are size and shape. The largest capsules are found in *Lopezia lopezioides*, *L. grandiflora*, *L. trichota*, whereas *L. gracilis* and *L. gentryi* have the smallest ones. Slight differences in size, however, have been observed between the members of related pairs of species such as *L. miniata* and *L. racemosa*, *L. nuevo-leonis* and *L. miniata*, *L. clavata* and *L. sinaloensis*. Several species are distinguished by the shape of their fruits: *L. clavata*, *L. sinaloensis*, *L. riesenbachia* with ± cylindrical capsules; *L. nuevo-leonis* with oblong-ellipsoid capsules; *L. cornuta* with angularly oblong-obovoid and horned at apex capsules; *L. gentryi* with setose-tubercled capsules and *L. laciniata* with obovoid-obconical ones. Most of the others have subglobose capsules.

The seeds of *Lopezia* are ballistically dispersed from the wind-shaken, open capsules. A few seeds remain at the bottom, and they just fall with or from the dry capsule. The seeds of *L. lopezioides* are narrowly winged, as if they might be adapted to anemochory, but they are so heavy and their wings so narrow that this scarcely seems possible.

In a few species such as *Lopezia trichota* and *L. semeiandra* the capsules have thick valves which sometimes dehisce tardily or do not open at all while still on the plant. In these cases the capsule is the dispersal unit and is presumably dispersed by streams.

Seeds.—Species of *Lopezia* are often distinguished sharply by the texture of their seeds. In *L. grandiflora*, *L. longiflora*, and *L. langmaniae* the seeds are coarsely long-tubercled; in *L. trichota*, *L. smithii*, *L. cornuta*, and *L. nuevo-leonis* they are also coarsely tubercled but with rounded tubercles; the seeds of other species are ± finely tubercled. The tubercles or papillae are transversely arranged in *L. conjugens*, *L. riesenbachia*, and *L. sinaloensis*, ± so in *L. racemosa* subsp. *moelchenensis* and *L. nuevo-leonis*; they are longitudinal in *L. gracilis* and *L. semeiandra*. The seeds of *L. trichota* are transversely wrinkled and also somewhat marginate; in *L. lopezioides* the seeds are smooth and distinctly winged. *Lopezia lopezioides* also has the largest seeds in the tribe. Relatively large seeds occur in *L. longiflora* and *L. cornuta*; relatively small seeds are found in *L. miniata*, *L. ciliatula*, *L. riesenbachia*, *L. clavata*, and *L. laciniata*. No significant differences in shape have been observed.

Chromosome numbers.—When known, these are given in the present paper. Documentation for the chromosome numbers cited here will be given by Plitmann, Tai, and Raven (1974). Results of experimental hybridizations will likewise be reported in due course.

Relationships of the Tribe

One of the six tribes of Onagraceae (Raven, 1964), Lopezieae are sharply set off from all others by their 4-merous flowers and 2-merous androecium. Although the chromosomes of Lopezieae are unspecialized (Kurabayashi, Lewis & Raven, 1962) and some species retain the original basic chromosome number for the family Onagraceae, $n = 11$, Lopezieae do not appear closely related to Fuchsieae and even less so to Circaeeae, the other two tribes that have a similar chromosomal constitution. The traditional grouping of Lopezieae with Circaeeae (*e.g.* by DeCandolle, 1828; Spach, 1835; Baillon, 1877; and Raimann, 1893) seems to have to do with nothing more than their common possession of two stamens (Eyde & Morgan, 1973). Recently Eyde and Morgan (1973) have postulated a connection between Jussiaeeae and Lopezieae on the basis of their similar nectaries, unique in the family, and lack of a floral tube. Further studies of additional characteristics will help to elucidate these reticulate relationships, but their nature leads one to emphasize the rather isolated position of the tribe Lopezieae within the family.

Generic Limits

It has been traditional to recognize four genera—*Diplandra*, *Lopezia*, *Riesenbachia*, and *Semeiandra*—in the tribe Lopezieae (Endlicher, 1840, 1841; Bentham & Hooker, 1862; Raimann, 1893). In 1877, Baillon placed *Riesenbachia* and *Semeiandra* in the synonymy of *Lopezia*, retaining *Diplandra* as distinct. Although T. S. Brandegee (1889: 158) wrote in favor of such a generic alignment, apparently it has not been followed by other authors. In 1909, Rose described three additional ones: *Pelozia*, *Jehlia*, and *Pseudolopezia*. He segregated them from *Lopezia* largely on the basis of petal morphology and the degree of adnation and connation in the flower. In the most recent overall revision, Munz (1961) recognized *Diplandra*, *Lopezia*, *Riesenbachia*, *Semeiandra*, and *Pseudolopezia*, but not *Jehlia* or *Pelozia*. He frankly admitted that his decisions about the limits of genera were arbitrary, and that the matter needed further study. The next year Miranda (1962) reemphasized the distinctiveness of *Lopezia langmaniae* (Miranda, 1953) and argued for the recognition of *Jehlia*. Thus the question of generic alignments in Lopezieae has been a vexed one, with nearly every student of the group having a different opinion.

Our studies and particularly those of Eyde and Morgan (1973) have shed new light upon relationships within Lopezieae; Eyde and Morgan's findings are summarized in Fig. 11 (reprinted from Eyde and Morgan, 1973: 123). A table of the sections and species we recognize was given on p. 479. The most distinctive units within the tribe are *Lopezia lopezioides* (sect. *Diplandra*) and *L. semeiandra-L. riesenbachia* (sect. *Riesenbachia*; the genera *Semeiandra* and *Riesenbachia*). *Lopezia lopezioides* is the only member of the group that retains two fertile stamens; yet its flowers are highly zygomorphic, its ovules have been reduced to one per locule, and its stylar bundles are relatively indistinct. Its subopposite leaves may or may not be primitive, and it shares the original basic chromosome number of the group, $n = 11$, with several other species. On the other hand, *L. longiflora* (the section or genus *Pseudolopezia*), although it has only one fertile

stamen, has the most radially symmetrical flowers in the group, ones that might in all respects other than their androecial condition be considered most generalized. *Lopezia semeiandra* (the genus *Semeiandra*) and *L. riesenbachia* (the genus *Riesenbachia*) have virtually identical floral tubes, so much so that they must be considered to have had a common ancestor with a tube of this sort and the chromosome number which they share in common, $n = 9$. Despite this communality of features, the contrast between the large, red, hummingbird-pollinated flowers of *L. semeiandra* and the small, purplish, autogamous ones of *L. riesenbachia* is, as Eyde and Morgan (1973) have pointed out, rather startling. Their capsules and seeds differ markedly, and they occur in very different situations ecologically.

In view of these highly reticulate relationships, it seems to us that there is nothing to be gained by removing up to five monotypic genera (*Diplandra*, *Jehlia*, *Pseudolopezia*, *Riesenbachia*, and *Semeiandra*) from a small genus of 21 closely related species. *Pelozia* has been recognized as distinct only by its author (Rose, 1909) and by Sprague and Riley (1924), Riley (1924), and Willis (1966); other authors have followed the lead of M. E. Jones (1929) and declined to regard it as generically distinct. Floral evolution has evidently been rapid in this group, and adaptation to different pollination systems has resulted in the production of a number of superficially very different but fundamentally similar floral types within the group. We wish to emphasize the unity which binds together these species is a whole array of geographical, morphological, anatomical, and cytological features, and believe that to group them in a single genus is the preferable way of expressing the pattern of diversity in the tribe. Suggestions that Lopezieae may be polyphyletic (Baehni & Bonner, 1948) are certainly without merit, in the light of recent research. Less diversity characterizes the resulting group than is found in *Ludwigia*, *Camissonia*, *Oenothera*, *Fuchsia*, or even the ditypic *Gongylocarpus* as currently recognized. In *Lopezia*, there is an impression of greater diversity owing to the spectacular changes that have occurred in floral conformation in relation to specific pollination systems, enhanced by early trends toward zygomorphy in the group. Nevertheless, the overall impression is of a group of relatively closely related species in which an impressive degree of adaptive radiation, affecting mostly the flowers, has taken place.

THE DELIMITATION OF SECTIONS IN *LOPEZIA*

Earlier efforts to subdivide *Lopezia* have not been extensive, although Sprague and Riley (1924) recognized two groups—Unituberculatae and Bituberculatae—depending upon the number of glands on the upper petals. Most other authors have tacitly assumed that the six segregate genera deserved formal recognition when included within *Lopezia*, but few such groups have actually been given names.

It follows from the discussion given above and by Eyde and Morgan (1973) that *Lopezia lopezioides* (*Diplandra*); *L. semeiandra* and *L. riesenbachia* (*Riesenbachia*); and the group earlier segregated as *Pelozia* (including *L. clavata*, *L. sinaloensis*, *L. laciniata*, and *L. gentryi*) deserve recognition as distinct sections

within the genus. We have chosen to emphasize the extensive similarities in floral anatomy between *L. semeiandra* and *L. riesenbachia* by combining them within a single section, even though their differences in external morphology, pollination system, and ecology are great.

Most of the remaining species are relatively closely related, and it would be defensible to group them within a single variable section. Nevertheless, it appears reasonable to segregate as sect. *Jehlia* (including *Pseudolopezia*) the three species characterized by bird pollination, tubular red flowers, and a chromosome number $x = 11$, from the remainder, which are fly-pollinated or autogamous, have more strongly zygomorphic, rose-purplish, lavender, or white flowers in which the petals and sepals spread at right angles from the top of the ovary, and chromosome numbers of $n = 10$ (or 20), 9, 8, or 7.

Among the remaining 12 species of *Lopezia*, *L. gracilis* stands out in floral anatomy and morphology (Eyde & Morgan, 1973). It is highly autogamous, and shares with the distantly related *L. gentryi* the lowest gametic chromosome number in the genus, $n = 7$. Unlike the other 11 species, which are probably closely related and derived from a single common ancestor, *L. gracilis* does not exhibit the snapping phenomenon, and there is no reason to consider it derived from ancestors that did exhibit this mechanism for outcrossing. Similar reasoning applies to the four species of sect. *Pelozia*, in which the union of floral parts is much more advanced than in *L. gracilis*. We believe that the relationships of the latter species are best indicated by segregating it as a monotypic section, coordinate with sect. *Pelozia* and sect. *Lopezia* and with them representing the greatest degree of floral specialization in the genus.

In setting up these six sections within the genus *Lopezia*, we have attempted to follow the reasonable standards established for the genus *Clarkia* by Lewis and Lewis (1955). Each section consists of one or more demonstrably closely related species between which hybridization may be possible. We have not yet succeeded in obtaining intersectional hybrids within the genus *Lopezia*.

Geography, Ecology, and Phylogeny

A majority of the 25 taxa of *Lopezia* recognized in the present revision occur in the following four regions:

I. West slope of the Sierra Madre Occidental, south to its junction with the Trans-Mexican Volcanic Belt in Colima. Thirteen taxa occur in this area, of which ten are restricted to it.

II. Sierra Madre along the Pacific Coast from Colima to the Isthmus of Tehuantepec. Nine taxa, five endemic.

III. Nuclear Central America, principally Chiapas and Guatemala. Four taxa, two endemic.

IV. Sierra Madre Oriental and western slopes of the Chihuahuan Desert. Four taxa, two endemic.

Two taxa occur beyond the limits of these four regions. They are *Lopezia miniata* subsp. *paniculata*, restricted to El Salvador, Costa Rica, and Panama; and *L. clavata*, found in southern Baja California. Only four taxa occur in more

than one region: *L. miniata* subsp. *miniata*, *L. racemosa* subsp. *racemosa*, *L. semeiandra*, and *L. grandiflora* subsp. *macrophylla*.

Although species of *Lopezia* are distributed widely in almost all of the mountainous areas of Mexico from northern Sonora in the west and central Nuevo León in the east southward to the Isthmus of Tehuantepec, it seems clear that their chief region of diversification and evolution has been the mountainous areas along the Pacific Coast. The Sierra Madre Occidental and the coastal ranges south to Oaxaca have been elevated since the late Cretaceous, perhaps 70 million years ago (Schuchert, 1935; Malfait & Dinkelman, 1972), whereas much of the remainder of Mexico was under the sea until much more recently. There is no concrete evidence for the evolution of the Onagraceae before the Paleocene, perhaps 65 million years ago (Krutzsch, 1968; Muller, 1970; Eyde & Morgan, 1973). As bird pollination can be shown convincingly to be the primitive system in *Lopezia* (Eyde & Morgan, 1973), and in view of the doubtful existence of specialized flower-visiting birds before Neogene time (J. Cracraft, personal communication), it would be difficult to imagine the existence of *Lopezia* or its immediate ancestors before the start of the Miocene, perhaps 25 million years ago, if that early. By this time, there was ample scope for radiation in relation to the diverse habitats of the Sierra Madre Occidental and coastal ranges to the south, and a variety of mesic and temperate habitats in which to survive temporarily unfavorable climatic episodes.

One can assume with confidence that the spread of *Lopezia* south of the Isthmus of Tehuantepec was an event of the upper Tertiary or Pleistocene, and that the evolution of *L. miniata* subsp. *paniculata* (from *L. miniata* subsp. *miniata*) and *L. langmaniae* (from *L. grandiflora*-like ancestors) were events of the past few million years. Two species of the genus, *L. miniata* and *L. racemosa*, are extremely widespread and weedy; they have probably spread to occupy much of the total range of the genus only in the upper Pleistocene and more recently, in part because of the spread of swidden agriculture four to six thousand years ago.

Reviewing now the ecology of *Lopezia* in broad terms, we offer the following summary by habitat type:

I. Dry understory of pine-oak forests: *Lopezia grandiflora*, *L. hintonii*, *L. longiflora*, *L. lopezioides*, and *L. smithii*. It may be that *L. racemosa* and *L. miniata* are principally associated with this habitat, but they have now spread widely into other disturbed habitats at middle elevations.

II. Moist seeps and streambanks in pine-oak forest: *Lopezia cornuta*, *L. gentryi*, *L. gracilis*, and *L. laciniata*.

III. Grassland (páramo) and other open places in cloud forest: *Lopezia miniata* subsp. *paniculata*.

IV. Tropical deciduous forest, especially along ravines and in other protected places: *Lopezia ciliatula*, *L. clavata* (nearly to sea level), *L. conjugens*, *L. langmaniae*, *L. riesenbachia* (to sea level), *L. semeiandra*, *L. sinaloensis*, and *L. suffrutescens*.

V. Stony ravines in piñon-juniper woodland: *Lopezia trichota*.

Comparing this summary with Fig. 11 (from Eyde & Morgan, 1973), it becomes abundantly clear that the principal site of evolution of *Lopezia* has been the pine-oak forest of the Sierra Madre Occidental and Pacific Ranges southward in Mexico. Much of the evolution of species within the genus has been in relation to the exploitation of relatively xeric habitats along the margins of the range of the group. Many of the species occur in pine-oak forest at middle elevations. A number of the species found in the Sierra Madre Occidental and other Pacific Coast ranges are restricted to one or two localities, not more than 150 km apart. These include: *Lopezia ciliatula*, *L. conjugens*, *L. grandiflora* subsp. *grandiflora*, *L. hintonii*, *L. laciniata* subsp. *ovata*, *L. longiflora*, *L. sinaloensis*, *L. smithii*, and *L. suffrutescens*. Other taxa have somewhat wider ranges in this region—the widest is *L. semeiandra*, which extends for more than 700 km in the interface between the Tropical Deciduous Forest and the pine-oak woodlands from northern Sinaloa to the northern edges of the Río Balsas drainage in southern Michoacán—but the overall picture is one of local endemism, rapid evolution, and especially survival of unusual taxa on a very local basis.

Most species of *Lopezia* flower in the first half of the dry season (October to December), and many continue for two or three months beyond this time. The widespread, weedy, polymorphic *L. racemosa* often flowers in the latter half of the rainy season (August, September). It is thus modally distinct from the equally widespread and weedy *L. miniata*, with which it can be hybridized. In general, the species most characteristic of xeric habitats, such as *L. trichota*, *L. clavata*, and *L. sinaloensis*, flower toward the end of the rainy season. *Lopezia gracilis*, which grows at relatively high elevations toward the northern end of the range of the genus, likewise flowers at the end of the period of summer rainfall.

In general, the pattern of evolution in *Lopezia* seems to have involved the derivation of ecologically or geographically marginal species which are relatively uniform morphologically from more widespread, variable ones. From polytypic and relatively widespread species such as the present-day *Lopezia grandiflora*, *L. miniata* subsp. *miniata*, *L. racemosa* subsp. *racemosa*, and *L. laciniata* have been derived such relatively uniform ones as *L. langmaniae*; *L. miniata* subsp. *paniculata*, *L. cornuta*, and *L. ciliatula*; *L. racemosa* subsp. *moelchenensis* and *L. conjugens*; and *L. gentryi*. As will be detailed in the paragraphs that follow, and discussed further in the systematic portion of this paper, such changes have often been accompanied by aneuploid changes in chromosome number and also by increased autogamy. Such evolutionary patterns are common in flowering plants, and it has been pointed out for example by Fisher (1965) that species of a given group found on "unusual" substrates are often much less variable morphologically than their widespread relatives.

The evolution of *Lopezia nuevo-leonis* ($n = 8$) appears to have taken place in locally favorable habitats on the dry slopes of the Sierra Madre Oriental from ancestors similar to *L. miniata* ($n = 10$). Similar aneuploid changes in chromosome number in relation to the occupation of marginal habitats by annual taxa appear to have taken place in the evolution of *L. ciliatula* ($n = 9$) from *L. miniata* ($n = 10$) and of *L. gentryi* ($n = 8, 7$) from *L. laciniata* subsp. *ovata*

($n = 10$), as well as in the presumably earlier evolution of *L. gracilis* ($n = 7$) and *L. clavata* ($n = 9$) from unknown ancestors with higher chromosome numbers, probably $n = 10$. These changes are reminiscent of those so elegantly documented by Lewis and his colleagues (*e.g.* Lewis & Lewis, 1955; Lewis & Roberts, 1956; Lewis, 1962, 1973) for *Clarkia*, an unrelated annual genus of Onagraceae, tribe Onagreae, and found also in other groups of annual plants (Stebbins, 1950). They may also be analogous with those that were involved in the evolution of plants with $n = 10$ (ancestors of sect. *Lopezia*) from those with $n = 11$, early in the history of the genus; the evolution of $n = 9$ in *L. suffrutescens*, presumably from ancestors with $n = 10$; and the evolution of other plants with $n = 9$ (common ancestor of *L. semeiandra* and *L. riesenbachia*), thought to have been an evolutionary event of some antiquity.

Lopezia trichota is the most divergent species of sect. *Lopezia* in terms of its pattern of ecological adaptation. Its underground parts are extremely swollen and bulbous, and its annual stems wither completely early in the dry season. Its tardily dehiscent capsules seem to be spread along streams and by periodic flooding. This species, which was presumably derived from ancestors somewhat similar to *L. racemosa*, occurs on dry slopes on both sides of the Chihuahuan Desert.

The stoloniferous habit of *Lopezia laciniata* (sect. *Pelozia*) is an obvious adaptation to the moist, mossy seepages on the faces of cliffs that it inhabits. A similar habit—that of rooting at the nodes from decumbent branches—is also characteristic of *L. racemosa* subsp. *moelchenensis* (sect. *Lopezia*), which occurs on somewhat protected limestone cliffs in Chiapas and Guatemala. Like a few populations of *L. racemosa* subsp. *racemosa*, *L. racemosa* subsp. *moelchenensis* is polyploid, with $n = 20$. The only other consistently polyploid taxon in *Lopezia* is *L. longiflora*, with $n = 22$; its ancestors are unknown and presumably extinct.

Also deserving special comment is the species pair *Lopezia clavata* (southern Baja California) and *L. sinaloensis* (Sinaloa). The former is an autogamous annual that occurs in colonies in the arroyos and on protected slopes. Its flowers are quite variable, as might be expected in a colonial, autogamous species that presumably is rarely visited by insects. Unfortunately, its mainland relative, *L. sinaloensis*, is known only from the type collection. Until it can be rediscovered, it will be difficult to evaluate precisely the relationship between the two, a matter of considerable interest.

To summarize the pattern of evolution within *Lopezia*, the group seems to have originated during or shortly before the Miocene in the pine-oak forest of the Sierra Madre Occidental of Mexico. The derivation of fly-pollinated and autogamous species from bird-pollinated ancestors and the occupation of increasingly xeric habitats, as well as secondary ones, with the development of annual taxa, appear to have been major trends that occurred subsequently. Connation and adnation among floral parts and the development of increasingly zygomorphic flowers are among the morphological and anatomical trends that accompanied the phylogenetic elaboration of the group. Aneuploid reduction in chromosome number and, less frequently the appearance of polyploidy, have

occurred in the evolution of various taxa, apparently connected with the reduction of recombination in ecologically marginal situations.

Systematic Treatment

Lopezia Cav.

Lopezia Cav., Icon. 1: 12. 1791. Munz, Brittonia 13: 77. 1961; N. Amer. Fl. II. 5: 15. 1965.

Pisaura Bonato, *Pisaura automorpha* e *Coreopsis formosa*, piante nuove. Padova, p. 12. 1793.

Riesenbachia Presl, Rel. Haenk. 2: 36, *t. 54*. 1831. Type: *R. racemosa* Presl = *Lopezia riesenbachia* Plitmann, Raven & Breedlove. Munz, Brittonia 13: 76. 1961; N. Amer. Fl. II. 5: 15. 1965.

Semeiandra Hook. & Arn., Bot. Beechey's Voy. *pl. 59*. 1836; 291. 1838. Type: *S. grandiflora* Hook. & Arn. = *Lopezia semeiandra* Plitmann, Raven & Breedlove. Munz, Brittonia 13: 74. 1961; N. Amer. Fl. II. 5: 14. 1965.

Diplandra Hook. & Arn., Bot. Beechey's Voy. *pl. 60*. 1836; 291. 1838. Nom. cons. prop., Raven & Plitmann, Taxon 20: 648. 1971, Taxon 22: 155. 1973; *non* Bertero, 1830, *nec* Rafinesque, 1840. Type: *D. lopezioides* Hook. & Arn. = *Lopezia lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 13. 1965.

Pelozia Rose, Contr. U. S. Natl. Herb. 12: 295. 1909. Type: *P. laciniata* Rose = *Lopezia laciniata* (Rose) M. E. Jones.

Pseudolopezia Rose, Contr. U. S. Natl. Herb. 12: 296. 1909. Type: *P. insignis* Hemsl. = *Lopezia longiflora* Decaisne. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 14. 1965.

Jehlia Rose, Contr. U. S. Natl. Herb. 12: 297. 1909. Type: *Lopezia macrophylla* Benth. = *L. grandiflora* Zucc.

Mostly well branched annual or perennial *herbs*, the perennials sometimes woody and with stems to 1 cm or more in diameter; plants often ± reddish; stems swollen or underground parts ± tuberous in some species. *Leaves* cauline, mostly spirally arranged, but sometimes opposite near the base or throughout in some species, reduced upward. *Stipules* present, small, mostly caducous. *Inflorescence* mainly terminal racemes, often leafy at base, more crowded toward apex, corymbose when young or at maturity in a few species, more rarely paniculate; bracts subsessile, narrowly lanceolate or linear, reduced leaves. *Flowers* many, borne on slender, long pedicels, slightly to markedly zygomorphic, often markedly protandrous; floral tube present or absent, the floral parts in any case somewhat united up to a constriction at the summit of the ovary. *Sepals* 4, subequal, narrowly lanceolate. *Petals* 4, subequal or unequal, the upper and lower pairs often markedly dissimilar, the upper 2 petals fused in some species (sect. *Pelozia*) with the upper 3 sepals for part of their length; petals red, purplish, lavender, or white. *Stamens* 2, the lower sterile in all except *L. lopezioides*; staminode petaloid, usually spatulate, ± enclosing the fertile stamen in many species, and releasing it explosively in sect. *Lopezia*; fertile stamen rotating in nearly mature but from its fundamentally introrse to a fundamentally extrorse position by the twisting of the filament near its end; stamens adnate to style in a few species; anther dorsifixed. *Pollen* blue, yellow in a few species (sects. *Pelozia*, *Riesenbachia*), shed singly. *Stigma* subcapitate, papillose at maturity. Ovary pluriovulate or with one ovule per locule in a few species. *Fruit* a loculicidal, 4-valved

capsule, subglobose or clavate, dehiscing at the apex. *Seeds* many, small, more or less tuberculate, or one per locule in a few species and then larger. Gametic chromosome numbers, $n = 7, 8, 9, 10, 11, 20, 22$; original basic chromosome number, $x = 11$.

TYPE SPECIES: *Lopezia racemosa* Cav.

Distribution: Nearly throughout Mexico and Guatemala, mainly at middle elevations, but absent from the northern deserts and lowland tropics; also in El Salvador, Costa Rica, and Panama.

KEY TO SECTIONS

1. Flowers with two fertile stamens; seeds narrowly winged, 3–4.5 mm long; leaves subopposite ..... Section I. *Diplandra*
1. Flowers with one fertile stamen and a staminode; seeds not winged, ca. 1(–2) mm long; leaves mainly alternate.
   2. Floral tube evident, the stamens and style united to one another and to the lower side of the floral tube ..... Section II. *Riesenbachia*
   2. Floral tube absent, the stamens and style not united except rarely at the very base.
      3. Upper three sepals connate at the base, the petals arising from them; constricted neck at summit of ovary prolonged ..... Section V. *Pelozia*
      3. Sepals not connate; constricted neck at summit of ovary not prolonged.
         4. Flowers bright red, 1 cm or more long; stems swollen just below ground level ..... Section III. *Jehlia*
         4. Flowers purplish, lavender, pinkish, or white, rarely as much as 1 cm long; stems not swollen below ground level in most species.
            5. Wiry-stemmed annual of the northern Sierra Madre Occidental; seeds one per locule; fertile stamen neither tightly enfolded by the staminode nor explosively discharged by it ..... Section IV. *Nannolopezia*
            5. Widespread annual or perennial herbs; seeds usually many per locule; fertile stamen tightly enfolded by the staminode and explosively discharged by it in all but a few populations ..... Section VI. *Lopezia*

KEY TO THE SPECIES

1. Flowers with two fertile stamens; seeds narrowly winged, 3–4.5 mm long; leaves subopposite ..... 1. *L. lopezioides*
1. Flowers with one fertile stamen and a staminode; seeds not winged, ca. 1(–2) mm long; leaves mainly alternate 2
   2. Floral tube evident, the stamens and style united to one another and to the lower side of the floral tube. 3
      3. Flowers (3.5–)4–8 cm long, bright red; soft-wooded shrub, mainly of the pine-oak forest but reaching the upper limits of the tropical deciduous scrub ..... 2. *L. semeiandra*
      3. Flowers less than 1 cm long, lilac-violet or purplish to bluish-pink; annual herb; relatively low elevations in tropical deciduous scrub ..... 3. *L. riesenbachia*
   2. Floral tube absent, the stamens and style not united except rarely at the very base 4
      4. Upper three sepals connate at the base, the petals arising from them; constricted neck at summit of ovary prolonged 5
         5. Upper petals laciniate, white with red veins; pollen blue; capsule obovoid-obconical or subglobose 6
            6. Stoloniferous perennials 1–6 dm tall; some leaves longer than 3 cm; sepals 3.5–7 mm long; capsule obovoid-obconical, more or less puberulent ..... 18. *L. laciniata*
            6. Annual herbs 0.6–2.5 dm tall; leaves shorter than 3 cm; sepals 3–4.5(–5) mm long; capsule subglobose, setose or setose-tuberculate ..... 19. *L. gentryi*
         5. Upper petals not laciniate, pink; pollen yellow; capsule subcylindrical 7
            7. Main leaves subentire; upper petals lanceloate; staminode ca. 5 mm long; capsule ca. 3 mm thick; seeds transversely tuberculate, black; Sinaloa ..... 21. *L. sinaloensis*

20. Upper petals without a conspicuous gland; seeds transversely rugose-tubercled; leaves mostly opposite; Sinaloa, Mexico ---- 15. *L. conjugens*

20. Upper petals with a conspicuous gland; seeds muricately tuberculate; leaves alternate, rarely a few opposite; widespread ---- 14. *L. racemosa*

Section I. **Diplandra**

Lopezia sect. *Diplandra* (Hook. & Arn.) Plitmann, Raven & Breedlove, comb. nov.

Diplandra Hook & Arn., Bot. Beechey's Voy. 291, *pl. 60*. 1838. Nom cons. prop., Raven & Plitmann, Taxon 20: 648. 1971; Taxon 22: 155. 1973; *non* Bertero, 1830, *nec* Rafinesque, 1840. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 13. 1965.

Virgate woody *perennial*, the stems swollen just below the level of the ground. *Leaves* mainly opposite, some of the lower ones alternate. Inflorescence terminal, corymbose in flower, racemose in fruit. *Flowers* strongly protandrous, the parts free. *Sepals* subequal, the upper 3 ascending-divergent. *Petals* red, the upper ones larger than the lower ones. *Stamens* both fertile, equal or the upper one shorter. *Anthers* introrse. *Nectaries* massive. *Pollen* pale violet-blue. *Capsules* subglobose, opening to the middle, with one seed in each locule. *Seeds* 4, broadly oblong, flattened, narrowly winged. Gametic chromosome number, $n = 11$.

Type species: *Lopezia lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove.

Distribution: Known only from the pine-oak-madroño forests of a few volcanic mountains in northwestern Jalisco and south and central Nayarit, Mexico, at elevations of 1400 to 2000 or 2500 m.

This highly isolated relict species is one of the most interesting in the family Onagraceae. It occurs only in a few localities in the Sierra Madre Occidental at its junction with the Trans-Mexican Volcanic Belt. It is unique within the Lopezieae in its possession of two fertile stamens.

1. **Lopezia lopezioides** (Hook. & Arn.) Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—Figs. 14–19.

Diplandra lopezioides Hook. & Arn., Bot. Beechey's Voy. *pl. 60*. 1836; 292. 1838. Munz, Brittonia 13: 76. 1961; N. Amer. Fl. II. 5: 14. 1965.

Stems 10–30 dm tall, hirsute to glabrescent. *Leaves* hirsute to hirtellous; lower leaves (3–)4–11 cm long and 1.1–3.2 cm wide, oblong-elliptic to lanceolate, cuneate or attenuate at base, acute or acuminate at the apex, infrequently obtuse or even retuse, serrate or serrulate, ciliolate, with 7–15(–20) veins on each side of

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Figures 14–19. *Lopezia lopezioides*.—14. Stem and inflorescence, × 0.5.—15. Flower, × 2.8.—16. Flower with one sepal and two petals removed, × 2.8.—17. Capsule, × 2.8.—18. Seed, adaxial view, × 2.8.—19. Seed, abaxial view, × 2.8. All from *Breedlove 8052* (DS).

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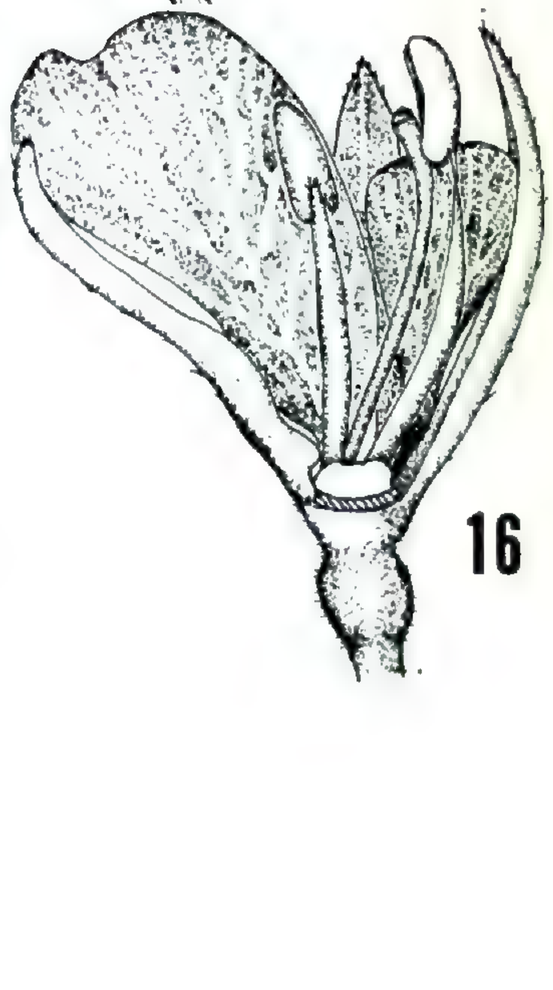

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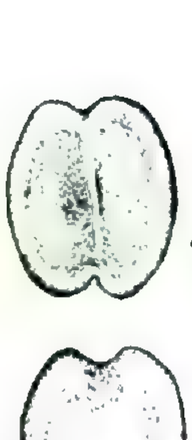

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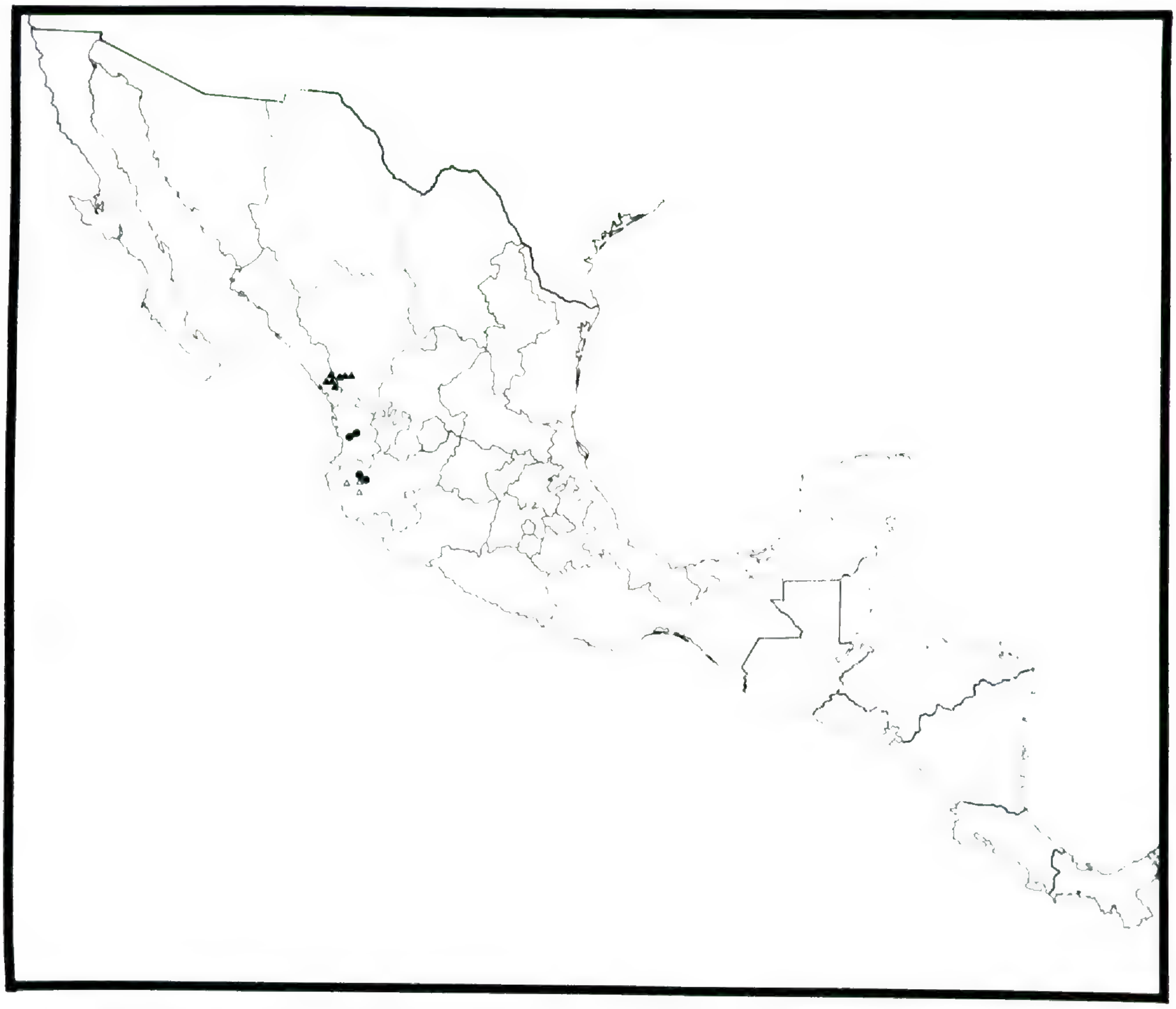


FIGURE 20. Geographical distribution of *Lopezia lopezioides* (dots), *L. laciniata* subsp. *laciniata* (open triangles), and *L. laciniata* subsp. *ovata* (filled triangles).

the midrib; upper leaves 0.9–3 cm long and 0.3–0.8 cm wide, lanceolate or linear-elliptic, acute to rounded at base, subacute at apex, serrulate to entire, with 5–10 veins on each side of the midrib; petioles 0–1.2 cm long. *Inflorescence* glandular-pubescent; pedicels 20–45 mm long, ascending or spreading, ± puberulent. *Sepals* 10–16 mm long, and ca. 2 mm wide, ± densely hirtellous and glandular-pubescent, the upper three ascending-divergent, the lower a little longer, somewhat incurved. *Petals* red, the upper ones 8–10 mm long and 4–5 mm wide, obovate, cuneate attenuate at base, truncate to retuse, the lower ones 4–7 mm long and 2–3 mm wide, oblong-oblanceolate, attenuate at base ± obtuse. *Stamens* 7–11 mm long; filaments 5–9 mm long; anthers 2.5–4 mm long. *Style* 5–9 mm long, ca. 0.5 mm thick; stigma ca. 1 mm in diameter; ovary 1.5–2 mm long, subglobose, puberulent. *Capsule* 7–12 mm long, 5–9 mm thick, puberulent to glabrescent; valves coriaceous, ovate, dentate-retuse at apex. *Seeds* 3–4.5 mm long, retuse at both ends. Gametic chromosome number, $n = 11$.

Type: Mexico, Nayarit, Tepic, 1827–28, *F. W. Beechey* (K; photograph, MICH).

Distribution (Fig. 20); known only from the pine-oak-madroño forests of a few volcanic mountains in northwestern Jalisco and south and central Nayarit, Mexico, 1400–2000(–2500) m elevation. Flowering, December to February or even April.

Additional specimens examined:
MEXICO. JALISCO: SW of Talpa de Allende, *McVaugh 14350* (MEXU, MICH, US), *23469* (MICH); Real Alto, Sierra Madre, *Mexia 1710* (A, BM, DS, F, GH, MICH, MO, S, UC, US). NAYARIT: Tepic, *Barclay 1170* (BM), *Jones 22872* (F, POM, US), *23546* (POM), *Palmer 1867* (BM, F, GH, US), *Paray 2716* (IPN, MEXU); Volcán de Sanganguëy, *Breedlove & Gregory 14225*, *Breedlove 7268*, *8052* (all DS). Locality unknown, *Walker-Arnott* (G, NY).

Pubescence, leaf size and serration, sepal and petal color, and to a lesser extent dimensions of the floral parts and capsule are all quite variable although this variation does not appear to be geographic.

Section II. **Riesenbachia**

Lopezia sect. *Riesenbachia* (Presl) Plitmann, Raven & Breedlove, comb. nov.

Riesenbachia Presl, Rel. Haenk. 2: 36, *t.* 54. 1831. Munz, Brittonia 13: 76. 1961; N. Amer. Fl. II. 5: 15. 1965.

Semeiandra Hook. & Arn., Bot. Beechey's Voy. *pl.* 59. 1836; 291. 1838. Type: *S. grandiflora* Hook. & Arn. = *Lopezia semeiandra* Plitmann, Raven & Breedlove. Munz, Brittonia 13: 74. 1961; N. Amer. Fl. II. 5: 14. 1965.

Annuals or slender woody *perennials*. *Leaves* subopposite or alternate. *Inflorescence* racemose or paniculate. *Flowers* red or purplish, strongly protandrous or autogamous, with an evident floral tube above the ovary, the tube divided by a median septum into two deep lateral pockets lined with nectariferous tissue which is massive or very limited. *Sepals* subequal, ascending or the three upper ones reflexed. *Petals* subequal or the lower ones broader, glandless. *Style*, stamen, and staminode united as a column and adnate to the lower side of the floral tube for about a third of its length, then separating from one another near the mouth of the tube. *Upper stamen* fertile, the lower one petaloid but not clasping the fertile one; upper end of filament of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. *Pollen* yellow. *Capsule* oblong-cylindrical or subglobose, open to middle or at apex only. *Seeds* many, small, muricate or rugose-tuberculate. Gametic chromosome number, $n = 9$.

TYPE SPECIES: *Lopezia riesenbachia* (Presl) Plitmann, Raven & Breedlove.

Distribution: Oak or oak-pine forests or tropical deciduous forests from the Sierra Surutato of Sinaloa of Michoacán and Guerrero, Mexico.

The superficial differences between the red-flowered, bird-pollinated *L. semeiandra* and the lilac-flowered, autogamous *L. riesenbachia* are most impressive, but the fundamental similarities that link them are even more so (Eyde & Morgan, 1973). It is reasonable to view *L. riesenbachia* as an autogamous derivative of the group which has evolved in marginal habitats at lower elevations and ranges farther southward. Probably *L. semeiandra* retains more of the ancestral features of this line.

2. **Lopezia semeiandra** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—Figs. 21–25.

Semeiandra grandiflora Hook. & Arn., Bot. Beech. Voy. *pl.* 59. 1836; 291. 1838. Munz, Brittonia 13: 74. 1961; N. Amer. Fl. II. 5: 14. 1965.

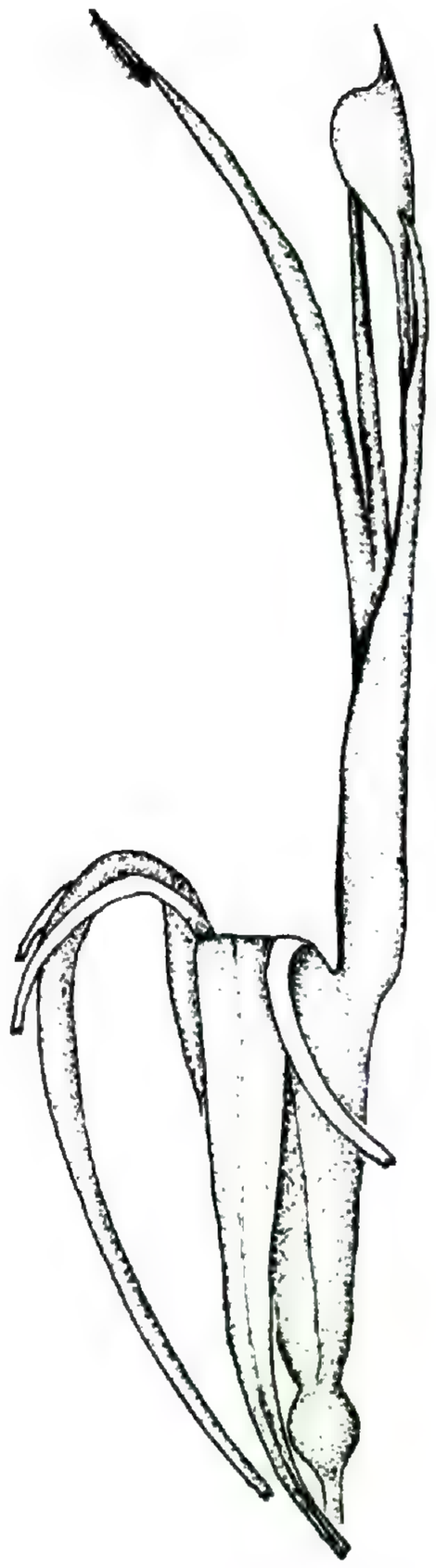
Hirsute woody *perennial*, with glandular and eglandular hairs. *Stems* 10–35 dm tall, well branched. *Leaves* 0.7–15(–17) cm long and 0.3–6.8 cm wide; lower leaves ovate to elliptic-oblanceolate, subacuminate at base, acute or acuminate at apex, serrate to serrulate-sinuate, with 14–27 veins on each side of midrib; upper leaves greatly reduced, much smaller, oblong-ovate to lanceolate, subacute at tip, serrate to entire, densely hirsute with viscid hairs, sometimes sericeous; petioles 0.1–2 cm long. *Pedicels* (5–)10–42 mm long, spreading, ± densely pubescent with spreading hairs. *Flowers* markedly protandrous, (3.5–)4–8 cm long; floral tube 14–20 mm long, bright red, hirsute inside. *Sepals* 15–45 mm long and 1–2 mm wide, red, ± hirtellous, the 3 upper reflexed, the lower one projecting forward. *Petals* 8–16 mm long and 0.5–1 mm wide, not clawed, linear, ± hairy outside toward base, red. *Fertile stamen* red, 30–60 mm long; anther 3.5–4 mm long. *Staminode* shortly obovate to boat-shaped and apiculate-cuspidate toward apex, red. *Style* 35–70 mm long, red, shortly and retrorsely hirsute; stigma 1–1.5 mm in diameter; ovary 2–3 mm long, ca. 2 mm thick, ovoid-subglobose, pubescent. *Capsule* 4.5–8 mm long, 3–6 mm thick, ovoid-oblong or subglobose, ± puberulent-hirtellous, bent upward when ripe; valves splitting apart to their middle, not recurved at apex. *Seeds* ca. 1 mm long, ovoid-oblong, incurved, muricate longitudinally with coarse tubercles. Gametic chromosome number, $n = 9$.

Type: Mexico, Nayarit, Tepic, 1827–28, *F. W. Beechey* (K, herb. Hook.; isotype, K, herb. Benth.; photograph, MICH).

Distribution (Fig. 26): Sierra Madre Occidental of Mexico, from the Sierra Surutato of Sinaloa south to Michoacán, chiefly in dry, open oak or oak-pine forests although occasionally in tropical deciduous forests with *Ipomoea*, *Ficus*, and *Bursera*, 400–1800 m elevation. Flowering, December to April.

Representative specimens examined:

Mexico. sinaloa: 19 mi. E of Río Concordia at Concordia, Rosario, *Breedlove 1618* (DS); 48 mi. E of Mocorito, *Breedlove 15619* (DS); Cañon Tarahumare, below La Jolla, Sierra Surutato, *Breedlove 15609* (DS); Capadero, Sierra Tacuichamona, *Gentry 5592* (DS, GH, MEXU, MICH, MO, NY, UC, US); 31 mi. E of Villa Union, *Wiggins 13171* (DS, MEXU, US); Balboa, San Ignacio, *Ortega 5048* (IPN, US), *1183* (Sec. Agric. Fom., MEXU); San Ignacio, *Ortega 294* (F, IPN), *404* (IPS); Tapiquahuis, San Ignacio, *Ortega 6855* (F, G, POM). durango: Chacala, *Goldman 343* (US); Sianori, *Ortega 5338* (IPN, MEXU, US); Sierra Tres Picos, *Gentry 5323* (DS, GH, MICH, MO, NY, US). nayarit: Volcán de Sanganguëy, E. of Tepic, *Breedlove 8068, 7269* (both DS); Tepic, Jones *23190* (GH, MO, NY, POM, UC, US), *Palmer 1910* (DS, F, G, GH, MICH, NY, S, UC, US, W), *Barclay 1163* (BM, RSA); Acaponeta, *Jones 22978* (F, POM, UC); Near Tepic, Cerro San Juan, *Paray 2698* (IPN, MEXU); N of Compóstela, *McVaugh 15295* (MEXU, MICH, RSA); SE of Ahuacatlán, *Feddema 320* (MICH, RSA); San Blas to Tepic, *Coulter 180* (K). jalisco: 12 mi. W of Autlán on Mex. Hwy. 80, *Breedlove 8070* (DS); 6 mi. W of Tecalitlán, *Breedlove 8073* (DS); San Sebastián, Sierra Madre Mts., *Mexia 1680* (A, BM, DS, F, G, GH, MICH, MO, NY, UC, US), *1415a* (UC), *1417* (US); El Colesio to Las Palmas, *Mexia 1320* (A, BM, DS, F, G, GH, MO, NY, UC, US, Z); Cerro Zapotlán (Ciudad Guzmán), *Reko 4665* (MEXU, US); SE of Nevado de Colima, *McVaugh 11797* (G, MEXU, MICH, RSA, US); Talpa to Mascota, *Nelson 4043* (GH, US); N of La Cuesta, *McVaugh 23346* (IPN, MICH); N-NE of Talpa de Allende,



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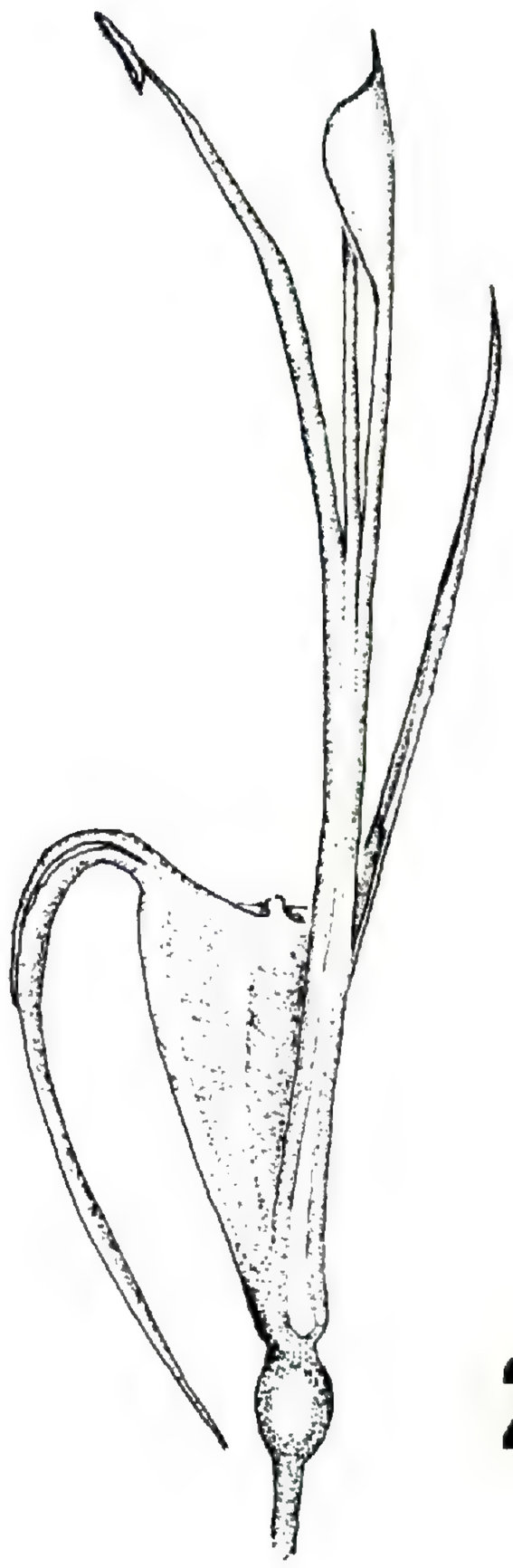

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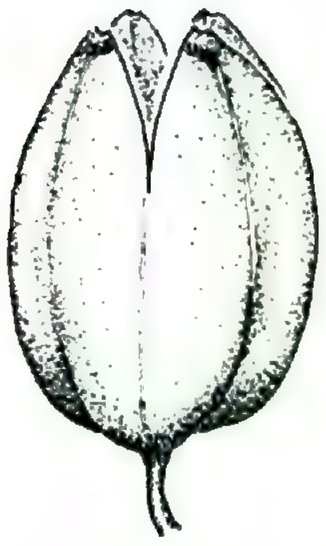

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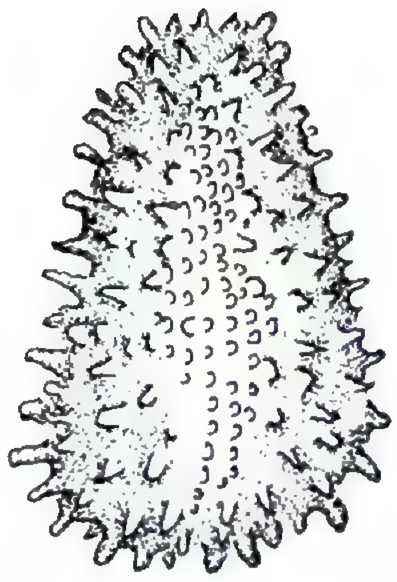

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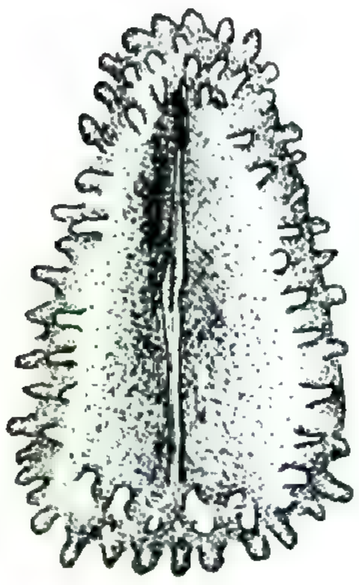

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FIGURES 21–25. *Lopezia semeiandra*.—21. Flower, × 10.—22. Median section of flower, × 12.—23. Capsule, × 5.—24. Seed, abaxial view, × 34.—25. Seed, adaxial view, × 34. Progeny of *Breedlove 1618* (DS).

McVaugh 20181 (MICH). COLIMA: Cofradia to San Antonio, Comalá, *Villerral de Puga 211* (DS, IPN). MICHOACÁN: Coalcomán, Sierra Torrecillas, *Hinton et al. 12742* (BM, DS, F, G, GH, K, MEXU, MICH, NY, P, POM, UC, US), *13670* (G, GH, NY, POM, TEX, US, W); Apatzingán, Aguililla, *Hinton et al. 15736* (BM, DS, F, MEXU, MICH, NY, POM, UC, US); Coalcomán, Sierra Naranjillo, *Hinton et al. 15783* (BM, DS, F, MEXU, MICH, NY, P, POM, UC, US), S of Arteaga, *McVaugh 22555* (IPN, MICH); NW of Aguililla, *McVaugh 22659* (IPN, MICH).

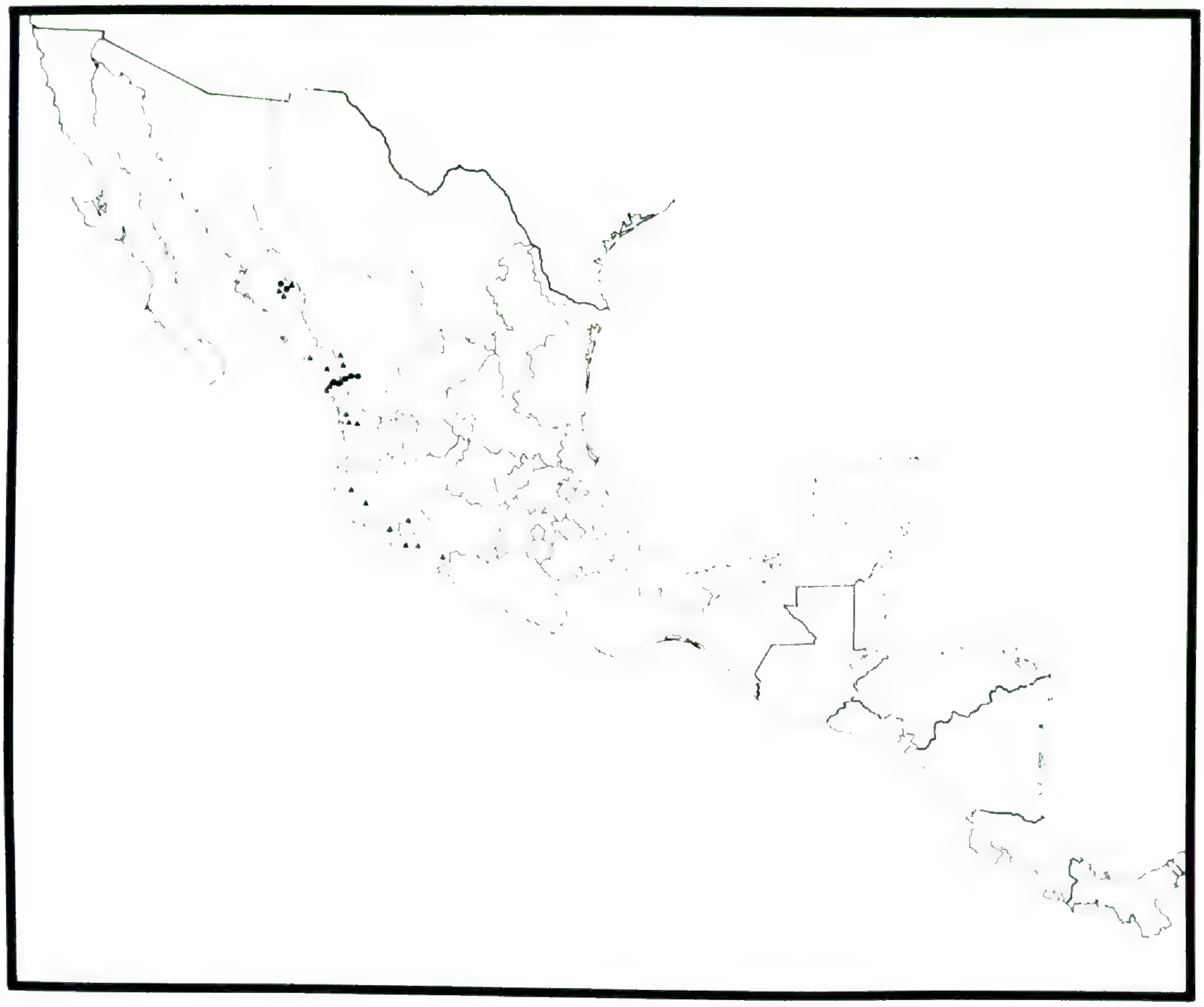

FIGURE 26. Geographical distribution of *Lopezia semeiandra* (triangles) and of *L. gentryi* (dots).

Lopezia semeiandra has been collected frequently during its flowering period in the dry season. Its variability is pronounced in: stature (length of stems); viscidity; dimension and serration of leaves; length of pedicels (extremely long in *Hinton 15736* from Michoacán and *McVaugh 15295* from Nayarit); length of sepals, stamens and style; and size of capsules.

3. **Lopezia riesenbachia** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—FIGS. 27–33.

Riesenbachia racemosa Presl, Rel. Haenk. 2: 36, *t.* 54. 1831. Munz, Brittonia 13: 77. 1961; N. Amer. Fl. II. 5. 1965.

Annual *herb*, rarely persisting a second year, densely strigulose to subglabrous, with an admixture of glandular pubescence. *Stems* 1.5–10 dm + all, ± erect.

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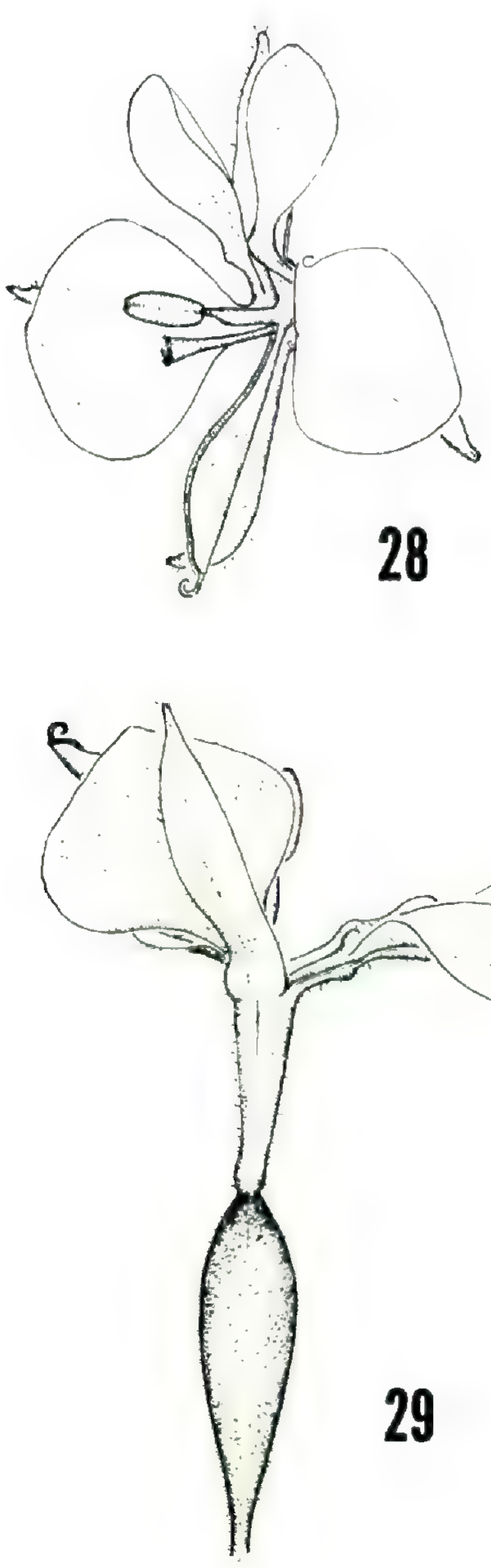
FIGURES 27–33. *Lopezia riesenbachia*.—27. Habit, × 0.53.—28. Flower, front view, × 5.3.—29. Flower, side view, × 5.3.—30. Flower, near median section, × 5.3.—31. Capsule, × 3.2.—32. Seed, abaxial view, × 42.—33. Seed, adaxial view, × 42. All from *Hinton 11652* (GH).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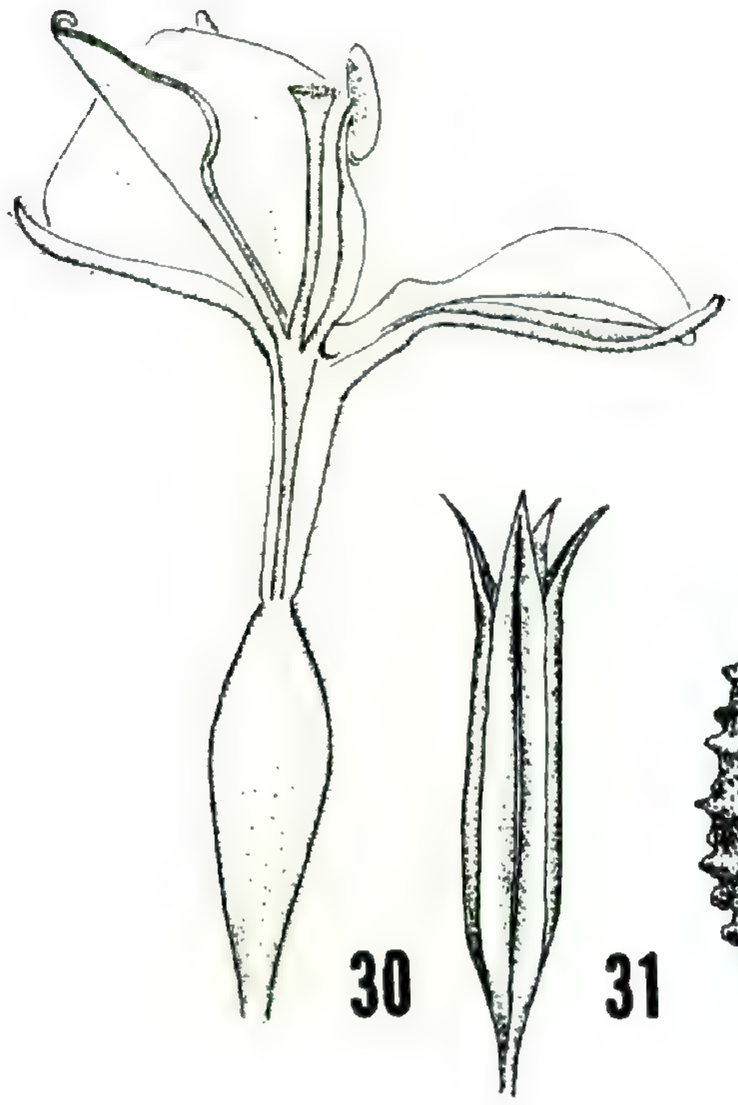
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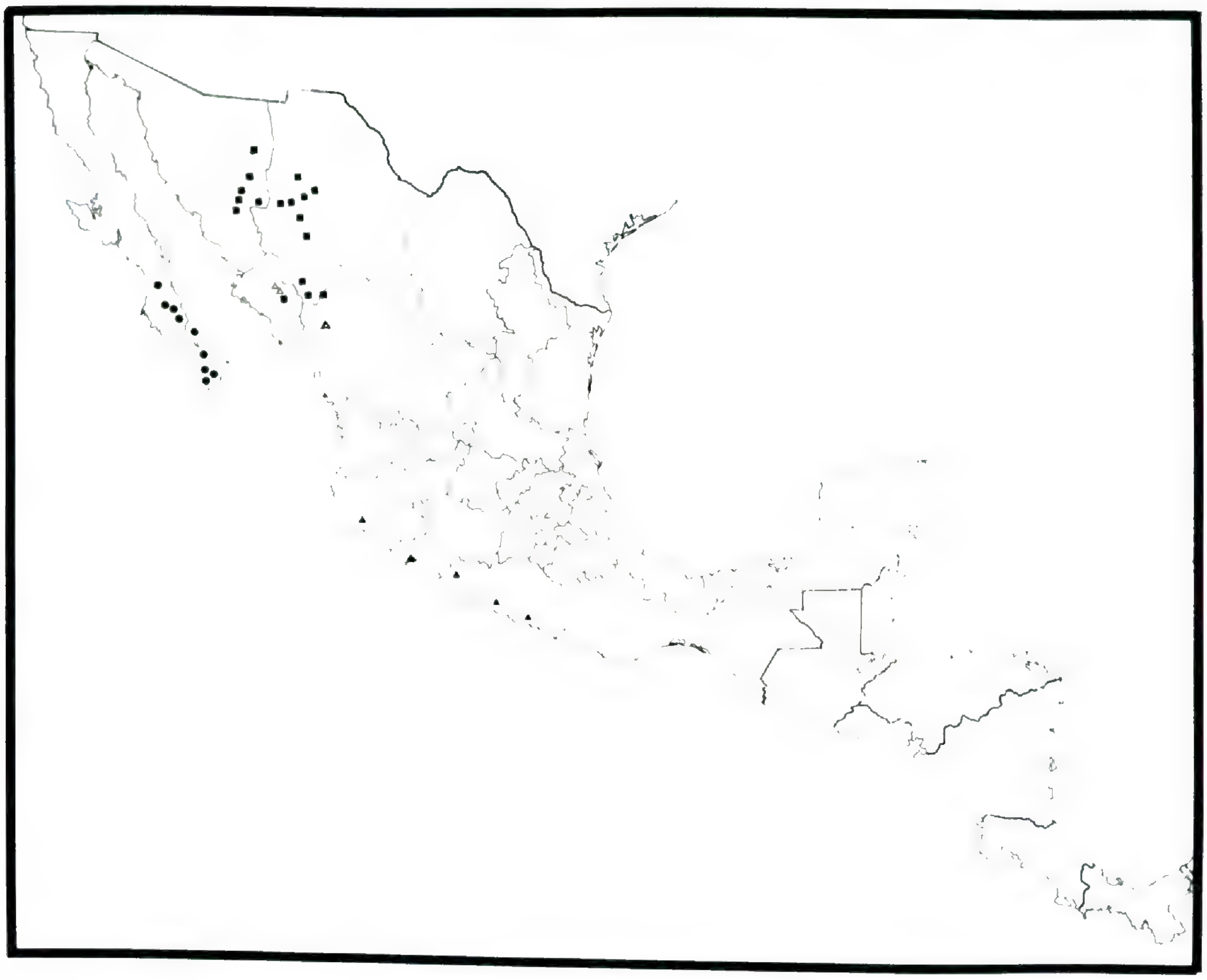


FIGURE 34. Geographical distribution of *Lopezia riesenbachia* (filled triangles), *L. gracilis* (squares), *L. ciliatula* (open triangles), *L. clavata* (dots), and *L. sinaloensis* (open box).

Leaves 0.6–12 cm long and 0.2–5 cm wide, ovate to oblong-oblanceolate, obtuse to cuneate at base, acute to acuminate at apex, the lower ones serrate, the upper ones ± serrate to subentire; petioles 0.15–3.5 cm long, very narrowly winged. Bracts densely strigulose to subglabrous; pedicels 5–12 mm long, ascending to erect, hirtellous. Autogamous. *Floral tube* 4–5 mm long, greenish or reddish, glabrous within. *Sepals* 3.5–5 mm long and 1–1.5 mm wide, hirtellous-pubescent, red or purplish, ± divergent. *Petals* cuneate or shortly clawed at base, lilac-violet or purplish to bluish-pink; lower petals 4–5 mm long and 2.5–4 mm wide, obovate, subacute to rotund at apex; upper petals 4–5 mm long and 1–2 mm wide, ± divergent, oblanceolate, subacute or obtuse at apex. *Fertile stamen* 3–5 mm long; anther 1.2–1.7 mm long, greyish-yellow, shedding pollen directly on the stigma at anthesis. *Staminode* 4–5 mm long, ovate to broadly spatulate, long tapering-clawed below, retuse at apex and with recurved subulate-apiculate tip, lilac, very rarely with a theca developed instead of half of limb. *Style* 3–5 mm long, filiform, somewhat dilated at base and toward stigma; stigma 0.9–1.7 mm in diameter, lilac; ovary ellipsoid, glandular-puberulent. *Capsule* 6–13 mm long, 1.5–3 mm thick, oblong-cylindrical, ± densely hirtellous-puberulent, erect;

valves thin, opening at apex only. *Seeds* small, ca. 0.5 mm long, transversely rugose-tubercled, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Guerrero, 1791, *Th. Haenke* (PR; photograph, RSA).

Distribution (Fig. 34): Sandy arroyos and rocky slopes in tropical deciduous forest associations in the foothills along the coast in Jalisco, Michoacán, Guerrero, and Oaxaca, Mexico, 100–1000 m elevation. Flowering, October to January.

MEXICO. JALISCO: 2 mi. W of La Huerta on Mex. Hwy. 80, *Breedlove 8071* (DS); N of El Rincón, *McVaugh 21027* (MICH). MICHOACÁN: Coalcomán, Huijontla, *Hinton et al. 12596* (DS, F, GH, K, MEXU, MICH, NY, US), *Hinton et al. 16133* (G, K, MICH, NY, S, UC, US), *16136* (G, K, MICH, NY, UC, US); Coalcomán, Áquila, *Hinton et al. 16297* (MICH, NY, US). GUERRERO: Montes de Oca, Vallecitos, *Hinton et al. 11652* (DS, F, GH, K, MEXU, MICH, NY, US), *11620* (GH, NY, US); Galeana (Atoyac), *Hinton et al. 10974* (DS, F, MEXU, MICH, NY, US); Cajinicuilar, *Langlassé 651* (G, GH, K, MICH, P, US); Acapulco, *Paray 2343* (IPN; peculiar form, more glandular than usual, capsules dehisce down to their middle), *Miranda 8433* (MEXU). OAXACA: Few km S of San Gabriel Mextepec, on road to Puerto Escondido, *Anderson & Anderson 5626* (MICH).

Lopezia riesenbachia is highly variable in the following: length, pubescence and color of stems; size and shape of leaves; shade of color of petals; dimensions of capsule. A particularly divergent specimen is *Paray 2343*, as noted above. In the field, flowering takes place during the first half of the dry season, from October to January, but in the greenhouse, it occurs two or three times a year without regard to day-length. This species is highly self-pollinated. Just as in *L. gracilis* and *L. laciniata*, the stamen is often only partly twisted around, and so deposits pollen directly on the stigma soon after the flower opens.

This species, collected in Guerrero in 1791 and described in 1831, was not seen again until 1898 and accurately described only in 1945 (Foster, 1945).

Section III. **Jehlia**

Lopezia sect. *Jehlia* (Rose) Plitmann, Raven & Breedlove, comb. nov.

Jehlia Rose, Contr. U. S. Natl. Herb. 12: 297. 1904.
Pseudolopezia Rose, Contr. U. S. Natl. Herb. 12: 296. 1909. [Type: *P. insignis* (Hemsl.) Rose = *Lopezia longiflora* Decaisne.] Munz, Brittonia 13: 75. 1961.
Lopezia subg. *Jehlia* (Rose) Munz, Brittonia 13: 77. 1961; N. Amer. Fl. II. 5: 16. 1965.

Virgate *subshrubs*, somewhat woody near the base, the stems swollen just below the level of the ground, sparsely branched. *Leaves* alternate or rarely sub-opposite in young growth. *Inflorescence* terminal, racemose. *Flowers* bright red, strongly protandrous, the parts free. *Sepals* subequal. *Petals* exserted or short and included within the tube formed by the sepals, the lower petals slightly larger than the upper ones. *Upper stamen* fertile, the lower one petaloid but not clasping the fertile one; upper end of filament of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. *Pollen* blue. *Capsule* oblong-ovoid to globose, open at the apex only or nearly to the middle. *Seeds* many, small, narrowly ovoid, roughly muricate with very prominent tubercles, brown. Gametic chromosome numbers, $n = 11, 22$.

TYPE SPECIES: *Lopezia grandiflora* Zucc. (*L. macrophylla* Benth.)

Distribution: Local and colonial in pine-oak forest and upper tropical deciduous scrub; eastern side of the valley of the Río Balsas, in states of México

and Morelos, Mexico, and from Oaxaca, Mexico, south into northern Guatemala, 900–2600 m elevation.

Although Miranda (1962) rightly emphasized the striking morphological differences between *Lopezia grandiflora* and *L. langmaniae*, Eyde and Morgan (1973) have shown even more impressive and fundamental similarities. Both of these species have more zygomorphic flowers than *L. longiflora*, but they are not otherwise remarkably different. All three species are hummingbird-pollinated, and they have relatively unspecialized flowers.

4. **Lopezia longiflora** Decaisne, Rev. Hortic. IV. 3: 221, *t. 30*, *fig. 12*. 1854.—Figs. 35–40.

Pseudolopezia longiflora (Decaisne) Rose, Contr. U. S. Natl. Herb. 12: 297. 1909. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 14. 1965.

Lopezia insignis Hemsl., Diagn. Pl. Nov. 1: 16. 1878. Hemsley, Biol. Cent. Amer., Bot. 1: 464, *t. 30*. 1880. Type: Mexico, *M. Bates* (K).

Pseudolopezia insignis (Hemsl.) Rose, Contr. U. S. Natl. Herb. 12: 297. 1909.

Virgate *perennial*, somewhat woody below, ± densely and finely pilose-hirsute. *Stems* to 40 dm tall, the tips drooping. *Leaves* 1.1–16.5 cm long and 0.3–10.5 cm wide; some of the lowermost, the uppermost and the youngest lower leaves larger than the upper, broadly ovate to oblong-lanceolate, with cuneate rather unequal base, acute or somewhat acuminate at apex, serrate or serrulate with glandular teeth, to 16 veins on each side of midrib, ± densely hirsute-pubescent with appressed hairs; upper leaves lanceolate to linear, cuneate at base, acute at apex, ciliolate and serrulate to entire at margins, with 10 or fewer veins on each side of midrib, sparsely hirsute-pilose to glabrescent; petioles 0.15–2 cm long. *Pedicels* 20–45 mm long, ascending to spreading, glabrous. *Flowers* nearly actinomorphic, to 4 cm long. *Sepals* 21–36 mm long and 2–4 mm wide, coherent when young, later almost distinct, sparsely pilose to glabrous, red. *Petals* linear-oblanceolate, narrowed toward base but not clawed, obtuse to acute at apex, glandless red; lower petals 27–35 mm long and 2–4.5 mm wide, somewhat involute, ± ciliate along the margins; upper petals 25–31 mm long and 1.5–3.5 mm wide, ascending-erect. *Fertile stamen* 36–50 mm long, anther 4.5–6 mm long, bluish. *Staminode* 35–45 mm long and 2–5 mm wide, generally spatulate, long attenuate at base, oblanceolately dilated or elongate at apex, emarginate and mucronulate, red. *Style* 40–50 mm long, reddish, filiform; stigma ca. 1 mm in diameter; ovary 15–23 mm long, 1–2.5 mm thick, ovoid-globose. *Capsule* 3.5–8 mm long, 3–6 mm thick, subglobose, splitting at apex only, glabrous. *Seeds* 1.3–2 mm long, ca. 1 mm thick. Gametic chromosome number, $n = 22$.

Type: Rev. Hortic. IV. 3: *t. 12*. 1854.—Described from the cultivated material illustrated, of which herbarium specimens are not known to exist. The seeds were collected in Mexico in September 1852 by M. Ghiesbreght.

Distribution (Fig. 41): Very restricted in range, although locally abundant in steep-walled volcanic barrancas along the upper part of the escarpment of the eastern side of the valley of the Río Balsas, Mexico, 1300–2000 m elevation. Some individuals are epiphytic (*Miranda 934*). Flowering, December to March.

7. Main leaves serrate or serrulate; upper petals oblong-spathulate; staminode to 3 mm long; capsule less than 2.5 mm thick; seeds finely tuberculate, brown; southern Baja California ..... 20. *L. clavata*

4. Upper three sepals not connate; constructed neck at summit of ovary not prolonged 8

8. Flowers bright red, 1 cm or more long; stems swollen just below ground level 9

9. Petals much shorter than the sepals, prominently tuberculate near the base, 3–5.5 mm long. ..... 6. *L. langmaniae*

9. Petals equalling or longer than the sepals, not or scarcely tuberculate, 7–36 mm long 10

10. Sepals and petals 2.6–3.6 cm long; stamens and style exserted, the fertile stamen 3.6–5 cm long ..... 4. *L. longiflora*

10. Sepals and petals 0.8–1.5 cm long; stamens and style included, the fertile stamen 0.6–1.8 cm long ..... 5. *L. grandiflora*

8. Flowers purplish, lavender, pinkish, or white, rarely as much as 1 cm long; stems not swollen below ground level in most species 11

11. Wiry-stemmed annual of the northern Sierra Madre Occidental; seeds one per locule; fertile stamen not tightly enfolded by the staminode and explosively discharged by it ..... 7. *L. gracilis*

11. Widespread annual or perennial herbs; seeds usually many per locule, rarely one; fertile stamen tightly enfolded by the staminode and explosively discharged by it in all but a few populations 12

12. Upper petals with two glands each, often auriculate 13

13. Upper petals conspicuously ciliate, 2.5–4 mm long; sepals 3–4.5 mm long ..... 12. *L. ciliatula*

13. Upper petals glabrous, 4–14 mm long; sepals 3.5–14 mm long 14

14. Sepals 6–14 mm long; lower petals 8–14 mm long, 5–9.5 mm wide; style 7–12 mm long; Sinaloa and Durango, Mexico ..... 9. *L. suffrutescens*

14. Sepals 3.5–9 mm long; lower petals 4–10 mm long, 1.5–6 mm wide; style 3–6 mm long; widespread 15

15. Capsule angular, horned at apex; pedicels drooping in fruit ..... 11. *L. cornuta*

15. Capsule rounded, not horned at apex; pedicels spreading or ascending in fruit 16

16. Leaves acutely serrate, fleshy; seeds black, very coarsely tubercled, ca. 1 mm long; Nuevo León and San Luis Potosí, Mexico ..... 10. *L. nuevo-leonis*

16. Leaves serrulate or subentire, not fleshy; seeds brown, finely tubercled, 0.6–1.5 mm long; widespread 17

17. Upper petals 7.5–10 mm long, obscurely auricled; sepals 6.5–9 mm long; seeds 1–1.5 mm long; Guerrero, Mexico ..... 7. *L. hintonii*

17. Upper petals 4–8 mm long, conspicuously auricled; sepals 3.5–7 mm long; seeds 0.6–1.2 mm long; widespread ..... 8. *L. miniata*

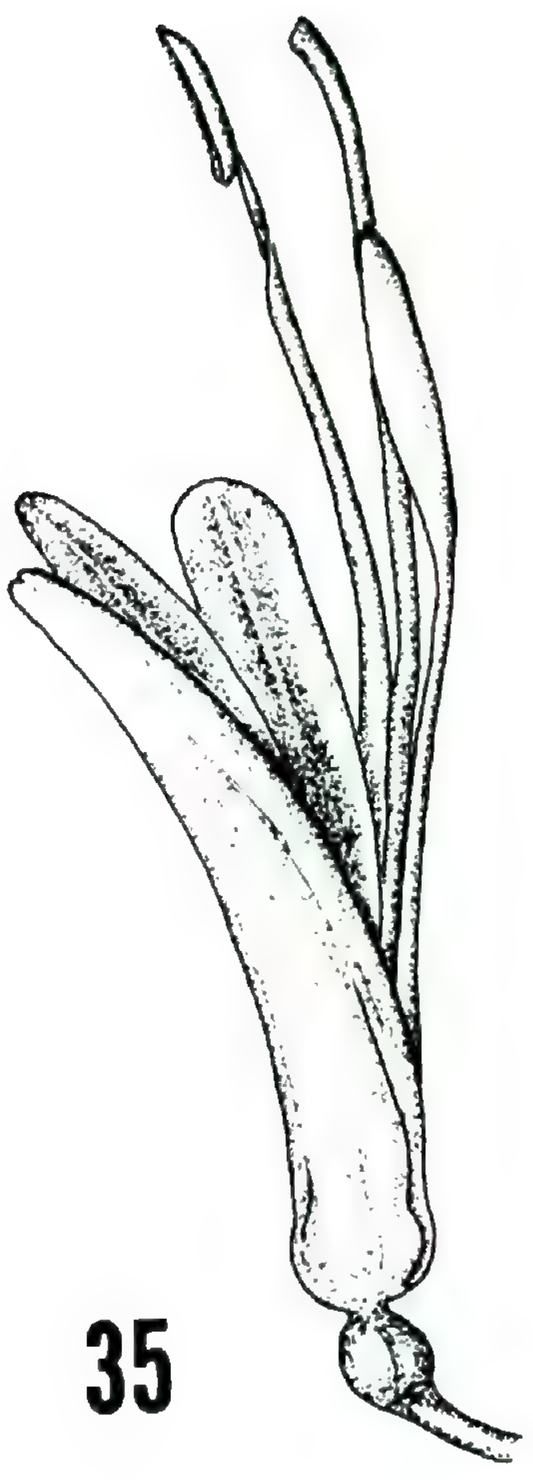
12. Upper petals with 1 gland each, or gland 0, not auriculate 18

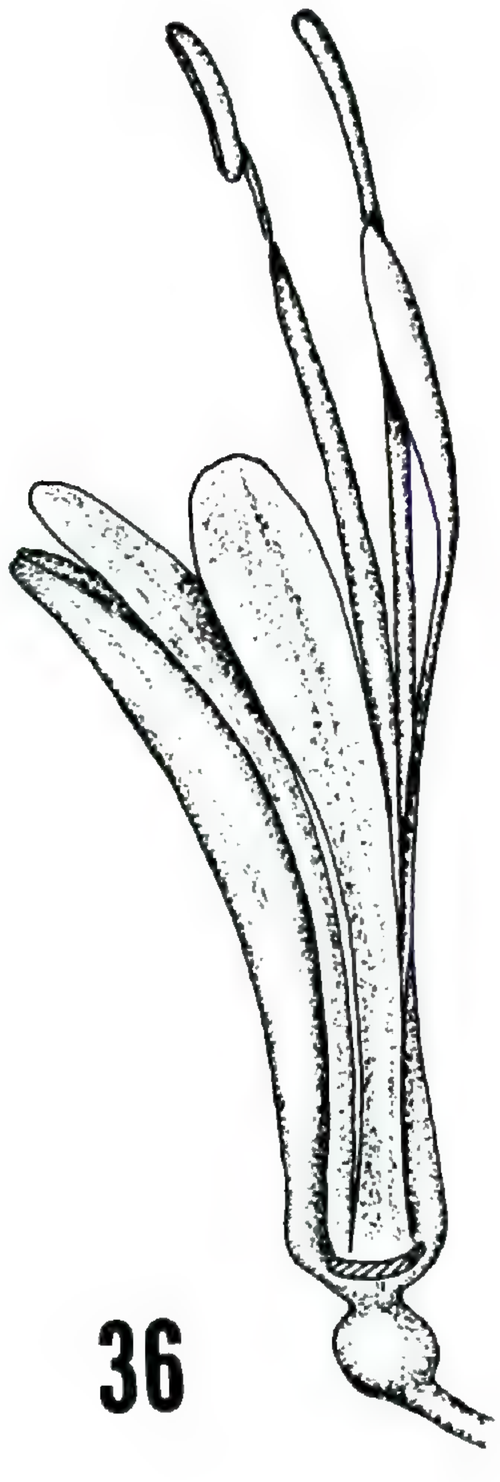
18. Petals long-ciliate, conspicuously bicolored, white above, purplish-red near the base; style crisp-pilose; roots tuberous, very thick ..... 13. *L. trichota*

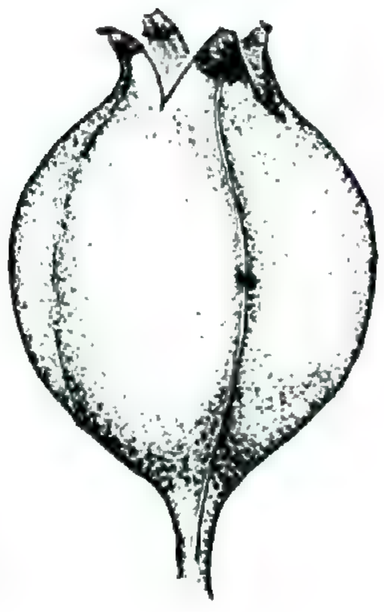
18. Petals not long-ciliate, not marked as above; style glabrous; roots not tuberous 19

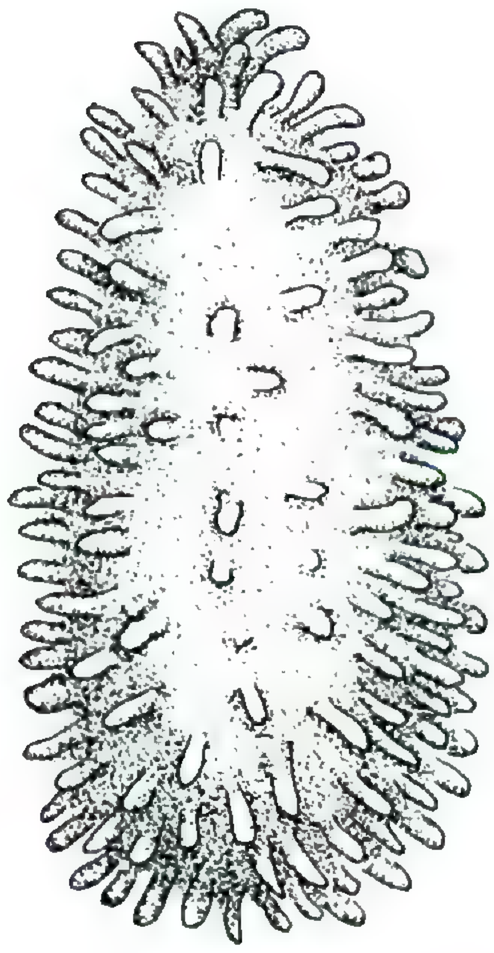
19. Portion of upper petals around the gland fringed with clavate hairs; leaves with subparallel edges near the base; sepals and petals mostly less than 5 mm long; Oaxaca, Mexico ..... 16. *L. smithii*

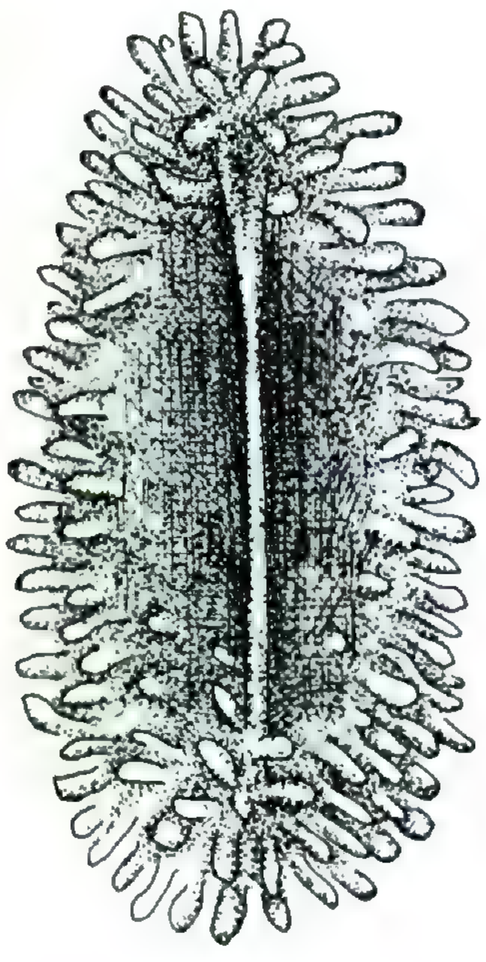
19. Upper petals not fringed with clavate hairs; leaves acute or obtuse at base; sepals and petals mostly more than 5 mm long; widespread 20











FIGURES 35–40. *Lopezia longiflora*.—35. Flower, × 1.4.—36. Flower with a sepal removed, × 1.4.—37. Dissection of base of flower, × 1.4.—38. Capsule, × 4.3.—39. Seed, abaxial view, × 28.—40. Seed, adaxial view, × 28. All from *Breedlove 8044* (DS).

Additional specimens examined:

MEXICO. MÉXICO: Ypericones, Temascaltepec, *Hinton 3896* (GH, MEXU), *3037* (BM, G, GH); Tejupilco, Temascaltepec, *Hinton 3662* (BM, G, GH, RSA, US). MORELOS: Trail to San José Laureles from Amatlán, *Miranda 934* (MEXU), *Breedlove 8044* (DS).

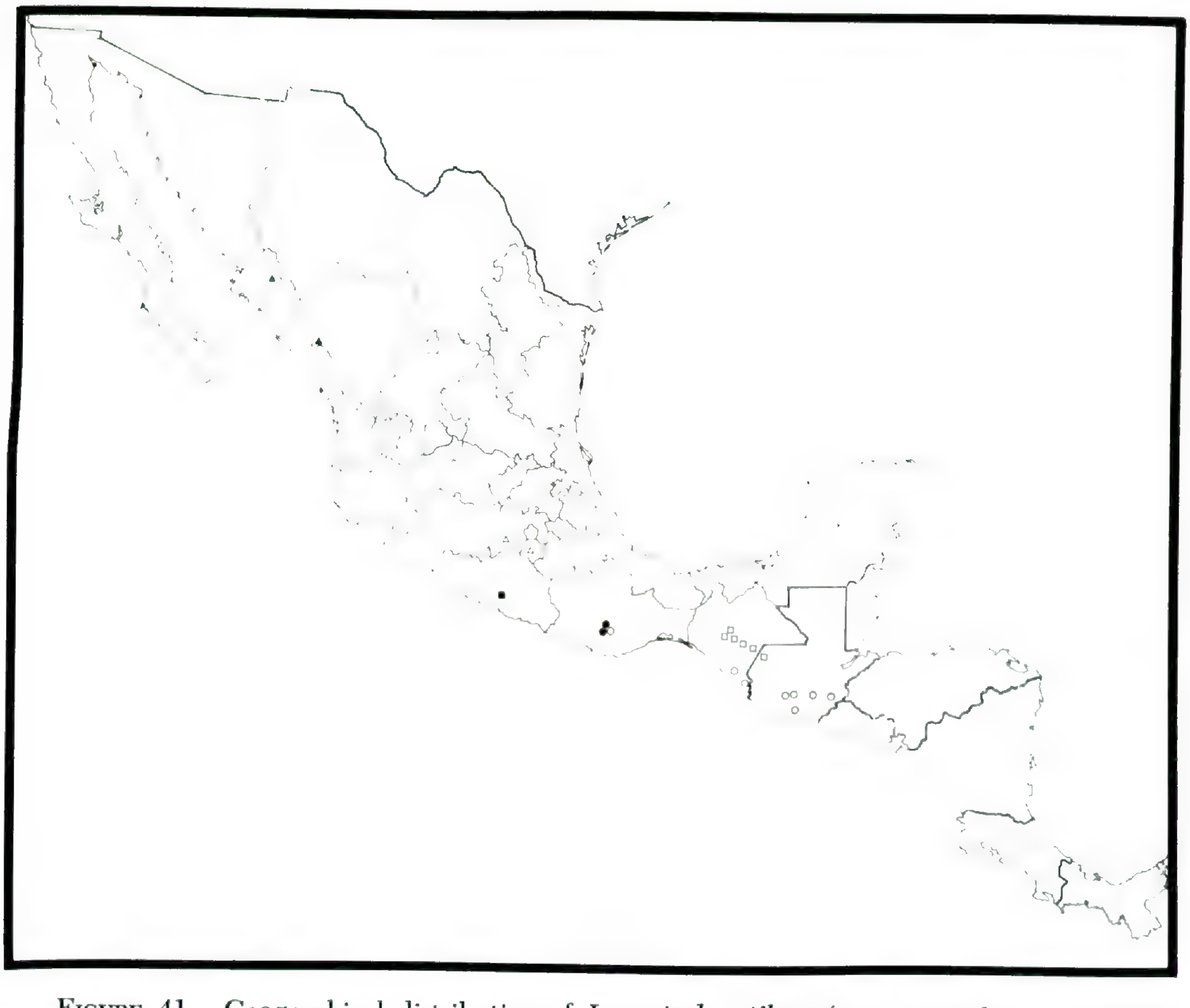


FIGURE 41. Geographical distribution of *Lopezia longiflora* (open triangles), *L. grandiflora* subsp. *grandiflora* (dots), *L. grandiflora* subsp. *macrophylla* (circles), *L. hintonii* (squares), *L. suffrutescens* (filled triangles), and *L. langmaniae* (open boxes).

5. **Lopezia grandiflora** Zucc., Flora 15, Beibl. 2: 101. 1832. Munz, Brittonia 13: 78. 1961; N. Amer. Fl. II. 5: 17. 1965.

Twiggy, densely strigulose to almost glabrous *shrubs*. Stems 10–20 dm tall; branches ± angular. *Leaves* serrate or serrulate; lower leaves ovate-elliptic to oblong, acute to rounded or asymmetrically cuneate at base, acute or acuminate at apex, densely or sparsely hirsute or strigose with 9–25 veins on each side of midrib; upper leaves narrowly ovate or lanceolate, subacuminate at base, acuminate or acute at apex, hirtellous or glabrous, with 6–15 veins on each side of midrib; petioles 0.15–3 cm long, somewhat dilated at base or even obscurely winged, shortly hirsute-pilose. *Racemes* strigose to subglabrous; bracts to 5 cm long; pedicels 10–55 mm long, ascending to erect, strigulose or subglabrous. *Sepals* 8–23 mm long and 1.5–3 mm wide, red, mostly subglabrous, ± ciliate-hairy at tip and sometimes along midrib. *Petals* red; lower petals 7–20 mm long and 4–8.5 mm wide, oblong-obovate to suborbicular, almost truncate to cuneate at base, very shortly clawed to subsessile, suborbicular or obtuse to subacute at apex, sparsely dentate, slightly erose or subcrenulate, sparingly strigulose or subglabrous, ± remotely and shortly ciliolate along the margins; upper petals

7–21 mm long and 2.5–5 mm wide, oblong to oblong-lanceolate, asymmetrical or not at the ± truncate (or subretuse) base of blade, very short-clawed, with or without 1–2 short projections, obtuse or subacute at apex, usually glabrous. *Stamen* 6–18 mm long, ± ciliolate at base to mostly glabrous; anther 2.5–6 mm long, red- or purplish-blue. *Staminode* 7–18 mm long, oblong-oblanceolate or linear-spatulate, narrowed or clawlike below but dilated at base, acute and shortly apiculate at apex, red. *Style* 6–17 mm long, finely hirsute toward base or subglabrous; stigma 1–1.5 mm in diameter; ovary ellipsoid or ovoid to globose, glabrous. *Capsule* 5.5–11 mm long, 4–9 mm thick, oblong-ovoid or subovoid to globose, somewhat reflexed to ascending, glabrous; valves dehiscing only near apex. *Seeds* 1–1.8 mm long, 0.7–1.1 mm thick. Gametic chromosome number, $n = 11$.

Distribution (Fig. 41): Pine-oak forests, scattered and colonial, from the Sierra Madre of Oaxaca, Mexico, south through Chiapas to central Guatemala, 1000–2000 m elevation. Flowering, late August to November.

Lopezia grandiflora consists of two subspecies, which differ mainly in quantitative characters. Zuccarini's original description of *L. grandiflora* is rather brief. The type specimen, from Oaxaca, is clearly the smaller-flowered northern subspecies, and not the southern one, as treated by Munz (1961: 78–9). It is thus an exact equivalent of the entity treated by Munz (1961: 79) as *L. galeottii*. Thus, the northern and narrowly restricted population is subsp. *grandiflora*, the wide-ranging and more common is subsp. *macrophylla*. The distinctions between these two subspecies are not clear-cut due to overlapping variation and the occurrence of morphologically transitional populations (*e.g. Purpus 6852* from Chiapas or *Miranda 399.S* from Oaxaca). Nevertheless, they are so distinctive that we believe they are best maintained, at least for the present, as distinct subspecies. Both are variable in size and pubescence of leaves, as well as in dimensions of floral parts and capsules. Munz (1961: 79) mentions *Seler 2655*, from Pueblo Viejo Quen Santo, Huehuetenango, Guatemala, as a peculiar felty form of this species; it is *L. langmaniae*.

KEY TO THE SUBSPECIES

Flowers 9–17 mm long; sepals 8–14(–15) mm long; lower petals 7–13 mm long ..... 5a. subsp. *grandiflora*

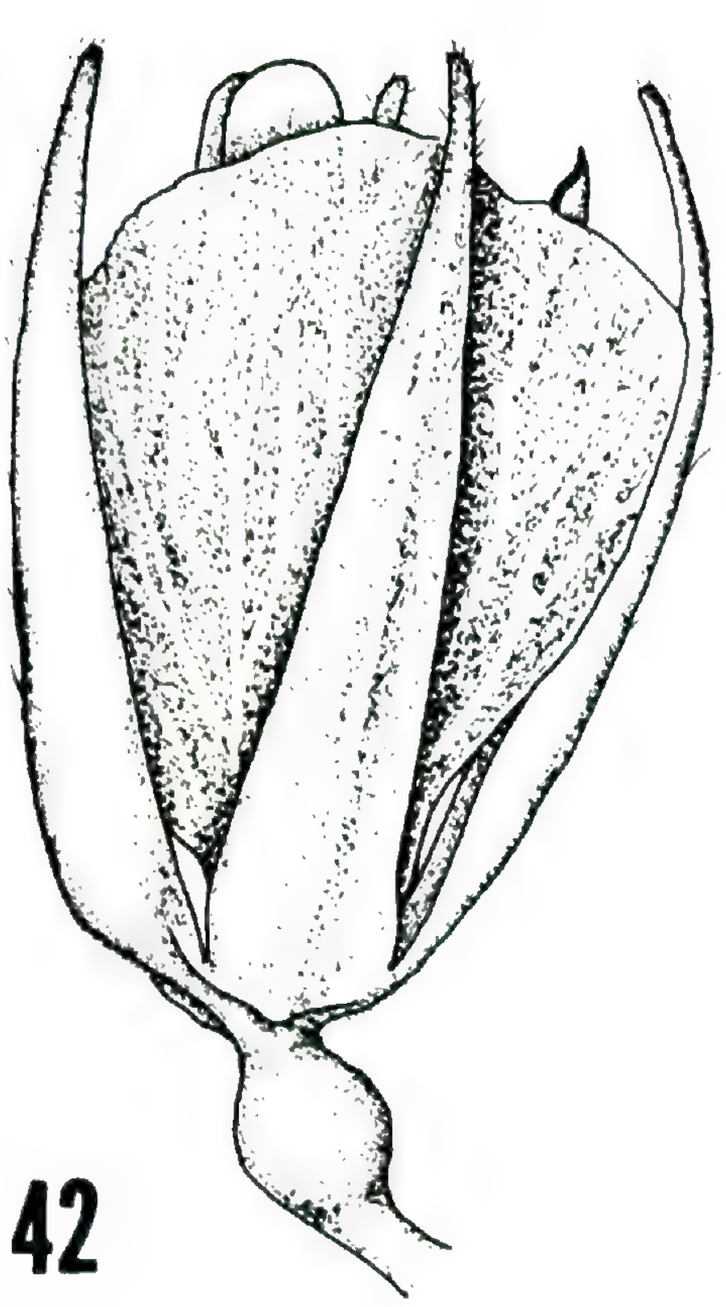
Flowers 16–26 mm long; sepals 14–23 mm long; lower petals 15–20 mm long ..... 5b. subsp. *macrophylla*

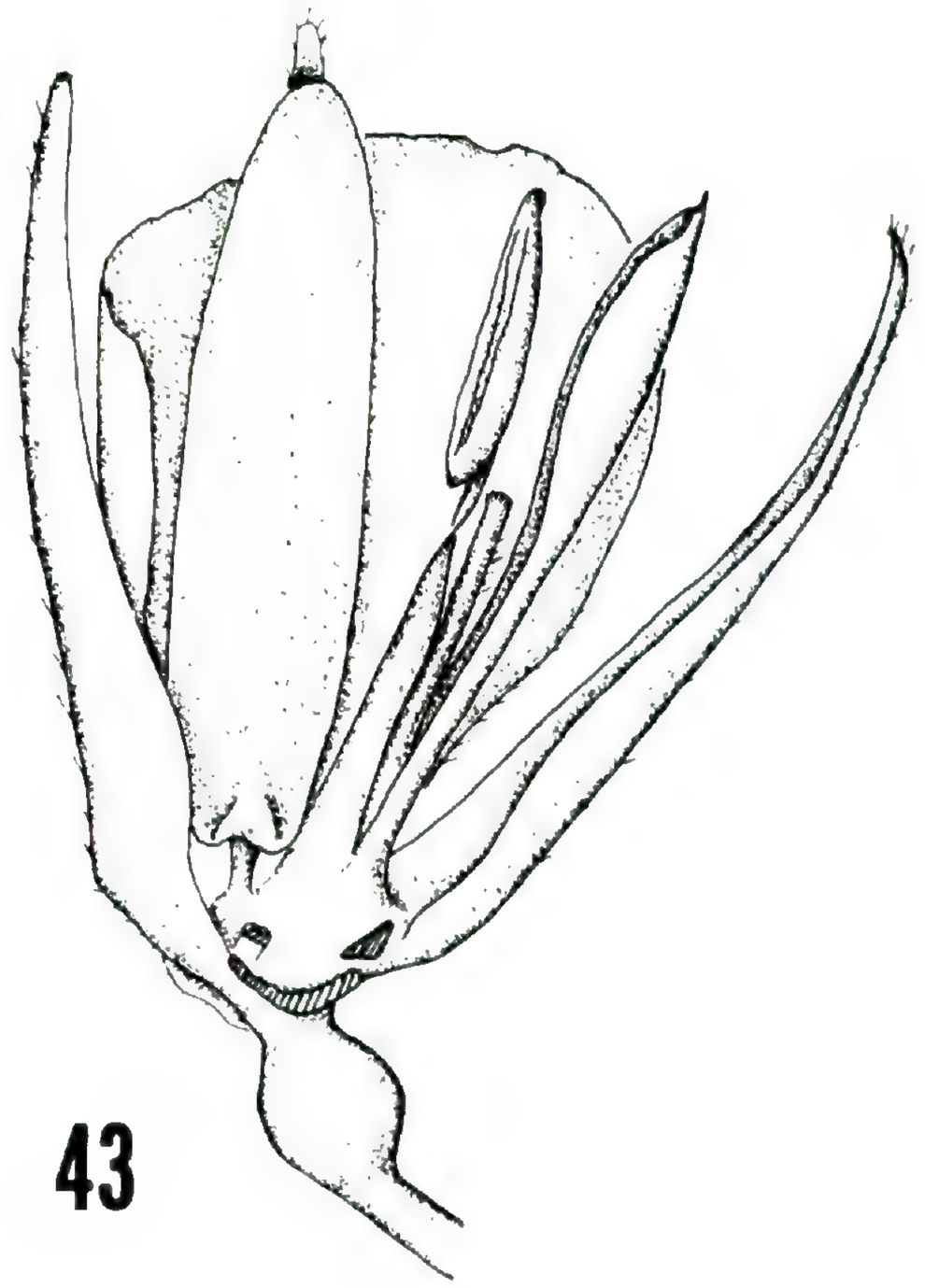
5a. **Lopezia grandiflora** Zucc. subsp. **grandiflora**.—FIGS. 42–47.

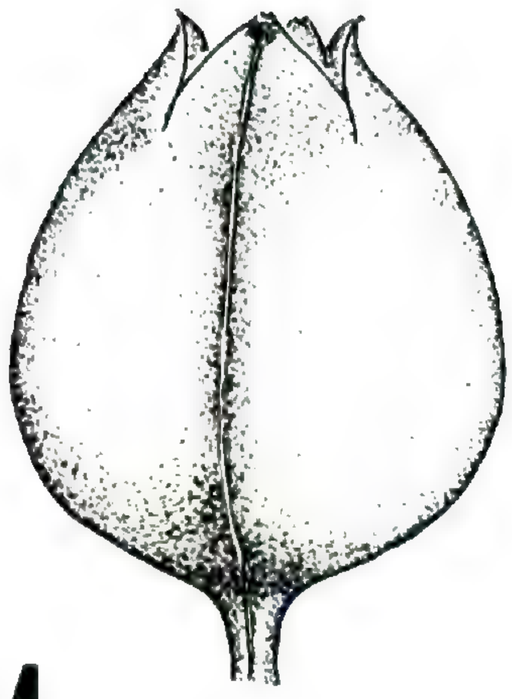
Lopezia galeottii Planch., Fl. Serres 7: 178. 1851–52. Type: Mexico, Oaxaca, calcareous rocks, 5–8000 ft. elevation, Nov.–April 1840, *H. Galeotti 2634* (P, lectotype, Munz, Brittonia 13: 79. 1961; K, P, isolectotypes; K, a plant with larger flowers; RSA, flower only; W, a single lower leaf 18 cm long and 5 cm wide, one capsule ca. 1 cm long). Munz, Brittonia 13: 79. 1961; N. Amer. Fl. II. 5: 17. 1965.

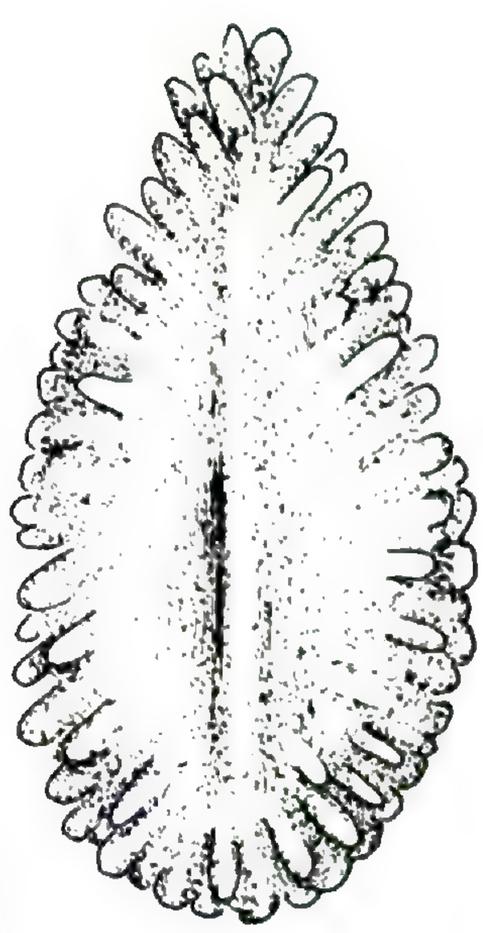
Jehlia galeottii (Planch.) Sprague & Riley, Jour. Bot. 62: 13. 1924.

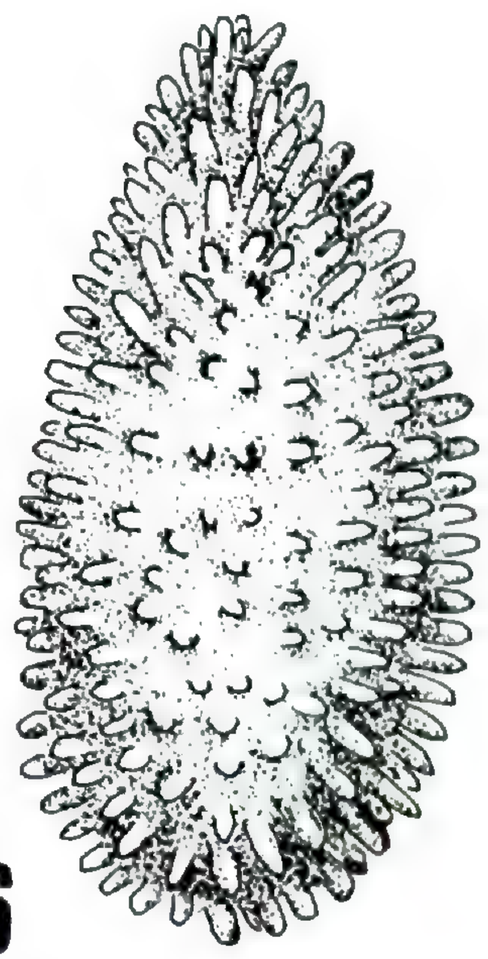
Leaves 5–11 cm long and 3–5(–6) cm wide, densely hirsute to glabrous, the lower ones with 9–14 veins on each side of midrib; petioles 0.2–2 cm long. *Pedicels* 1–3 cm long, puberulent. *Flowers* 9–17 mm long, rarely a little longer.











FIGURES 42–47. *Lopezia grandiflora* subsp. *grandiflora*.—42. Flower, × 3.8.—43. Near median section of flower, × 3.8.—44. Capsule, × 3.8.—45. Seed, adaxial view, × 24.—46. Seed, abaxial view, × 25. All from *Breedlove 7182* (DS).

Sepals 8–14(–15) mm long and 1.5–3 cm wide, subacute. Lower *petals* 7–13 mm long and 4–8 mm wide, upper petals 7–9 mm long and 3–4 mm wide, oblong-oblanceolate, obtuse. *Fertile stamen* 6–8 mm long; anther 2.5–5 mm long. *Staminode* 6–8 mm, oblong-oblanceolate. *Style* 6–7 mm long. *Capsule* 5.5–9 mm long, 4–7 mm thick. Gametic chromosome number, $n = 11$.

TYPE: Mexico, Oaxaca, Santiago el Grande, unplaced locality somewhere along the trail from Oaxaca to the Pacific Ocean, *via* Sola de Vega and Juquila, but on the Pacific slope; probably in the vicinity of Sola de Vega, whence come all other known collections. Original citation reads "Crescit in imperio mexicana prope Sant Jago el grande versus oceanum pacificum in sylvis densis, tierra templada (locis temperatis)," June–July, *C. de Karwinski* (M, herb. Zuccarini). Collected between 1827 and 1832.

Distribution (Fig. 41): Known only from the relatively open pine-oak forests N of Sola de Vega, Oaxaca, Mexico, 1500–1900 m elevation. Flowering, late August to November.

Additional specimens examined:
MEXICO. OAXACA: N of Sola de Vega, *Breedlove 7182, 7184, 12280* (all DS), *Miranda 3445* (MEXU), *Rzedwoski 21273* (DS, IPN, MICH, TEX).

5b. **Lopezia grandiflora** subsp. **macrophylla** (Benth.) Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.

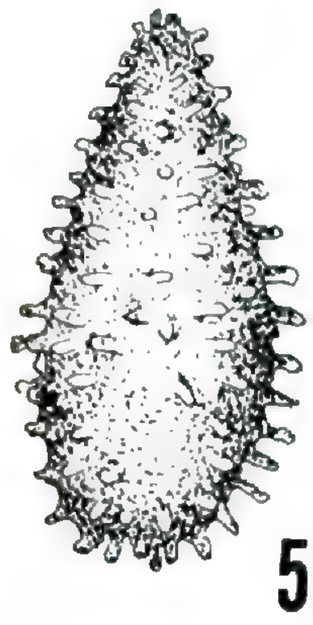
Lopezia macrophylla Benth., Pl. Hartw. 83, 92. 1841. Hooker, Curt. Bot. Mag. 79, IX: *t. 4724*. 1853.
Lopezia macrantha Benth. *ex* Regel, Schweiz. Zeitschr. Gartenbau 8: 25. 1850. (Misprint; *L. macrophylla* in the index.)
Jehlia grandiflora (Zucc.) Rose, Contr. U. S. Natl. Herb. 12: 297. 1909. Miranda, Brittonia 14: 46. 1962.
Jehlia macrophylla (Benth.) Rose, Contr. U. S. Natl. Herb. 12: 297. 1909.

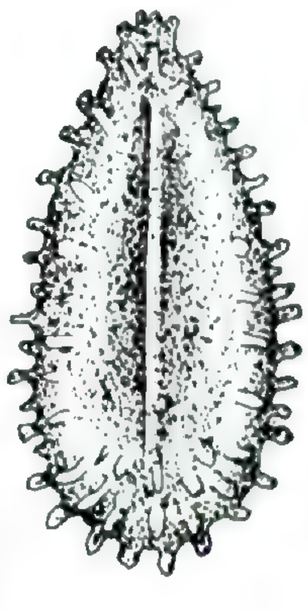
Leaves 0.9–16 cm long and 0.15–6.5 cm wide, usually ± strigose, the lower ones with 10–25 veins on each side of midrib; petioles 0.15–3 cm long. *Pedicels* 20–55 mm long, sparsely strigose to subglabrous. *Flowers* 16–26 mm long, rarely a little shorter. *Sepals* 14–23 mm long and 1.5–2.2 mm wide, angustate. Lower *petals* 15–20 mm long and 6–8.5 mm wide, subacute to obtuse at apex, elliptic-ovate to obovate; upper petals 16–21 mm long and 2.5–5 mm wide, oblong to oblong-lanceolate, subacute. *Fertile stamen* 15–18 mm long; anther 4.5–6 mm long. *Staminode* narrowly spatulate. *Style* 14–17 mm long. *Capsule* 6–11 mm long, 5–9 mm thick. Gametic chromosome number, $n = 11$.

TYPE: Guatemala, Sacatepéquez, "in summo jugo inter Dueñas et Acatenango ad pedem montis ignivomi" (SW of Antigua, near the foot of the twin volcano Acatenango-Fuego), 1840, *T. Hartweg 577* (K, lectotype, Munz, Brittonia 13: 79. 1961; isolectotypes, BM, G, NY, P, POM, US, W).

Distribution (Fig. 41): Pine-oak forests on the Pacific slopes of the Sierra Madre of Chiapas, Mexico, and on several of the volcanoes of north and central Guatemala, 1000–2700 m elevation. Once collected in the Sierra Madre of Oaxaca, Mexico. Flowering, late August to November.

Additional specimens examined:
MEXICO. OAXACA: 15 km S of Sola de Vega, *Rzedowski 21299* (greatly resembling this subspecies, although collected in the area of subsp. *grandiflora*; no other specimens known from Oaxaca; DS, IPN). CHIAPAS: San Pedro Alto, *Liebmann 3228* (GH, UC); Santa Rosa, Escuintla, *Matuda 17848* (F); Barranca Honda, Siltepec, *Matuda 4118* (DS, MEXU, MICH, NY); Cerro Boquerón, *Purpus 6852* (transitional to subsp. *grandiflora*; BM, F, GH, MO, NY, UC, US); Volcán Tacaná, *Matuda 2407* (A, F, MEXU, MICH, NY, US).
GUATEMALA. SOLOLA: Between Solola and Panajaches, *Degener 26620* (stems and leaves hirsute, grayish-green; US). CHIMALTENANGO: Calderas, *Johnston 1528* (F). SACATEPÉQUEZ:





FIGURES 47–52. *Lopezia langmaniae*.—47. Flower, × 3.5.—48. Near median section of flower, × 3.5.—49. Upper petal, × 3.5.—50. Capsule, × 3.5.—51. Seed, abaxial view, × 24.—52. Seed, adaxial view, × 24. All from *Breedlove 7161* (DS).

Volcán de Fuego, *Salvin*, 1873 (K, W); Volcán Acatenango, *Shannon & J. D. Smith 3649* (F, US). SANTA ROSA: Narango, *Heyde & Lux 3964* (G, GH, K, M, NY, POM, US). CHIQUIMULA: Cerro Brujo, *Steyermark 30964* (F); SE of Concepción de las Minas, *Steyermark 30915* (F). Without definite locality: *Heyde 348* (US), *Salvin* (K).

6. **Lopezia langmaniae** Miranda, Anal. Inst. Biol. Mex. 24: 88, *fig.* 9. 1953. Miranda, Brittonia 14: 46. 1962; Munz, N. Amer. Fl. II. 5: 17. 1965.—FIGS. 47–52.

Shrubby, ± densely silky-hirsute *perennials*, the hairs appressed or spreading. Stems few, 5–20 dm tall. *Leaves* 0.9–20 cm long and 0.15–8 cm wide, silky-pubescent; lower leaves oblong or elliptic, attenuate or cuneate at base, acute-apiculate at apex, ± serrulate, densely silky, with 15–24 veins on each side of midrib; upper leaves elliptic to narrowly lanceolate, subcuneate at base, acute or rarely obtuse at apex, subentire, less hairy, with 5–14 veins on each side of midrib; petioles 0.1–2 cm long and 0.1–0.25 cm wide, densely hairy. *Bracts* to 2 cm long and 1 cm wide; pedicels 14–30 mm long, ± ascending, ± pubescent. *Sepals* 11–17 mm long and 1–3 mm wide, 3 of them connate for 2–3 mm near the base, silky-pubescent. *Petals* whitish; lower petals 4–5.5 mm long and ca. 1.5 mm wide, linear to oblong-oblanceolate, acute to obtuse at apex, shortly clawed; upper petals 3.5–4.5 mm long and ca. 1 mm wide, varying in size and shape, more or less linear, clawed for ⅓–½ of their length, subacute at apex, broad and somewhat constricted at the middle, with gland at base of limb. *Fertile stamen* 16–22 mm long; filament ± compressed, the anther 2–3 mm long. *Staminode* 15–18 mm long, 2–3.5 mm wide, spatulate and long-clawed, retuse at apex and sometimes mucronate or rarely bearing a small reduced pale

anther, reddish. *Style* 15–21 mm long, subglabrous; stigma ca. 1 mm in diameter; ovary 1.5–2.5 mm long, 1.5–2 mm thick, pubescent. *Capsule* 4–8 mm long, 3.5–6 mm thick, subglobose to ovoid, somewhat appressed hairy-tuberculate. *Seeds* ca. 1.2–1.5 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 11$.

TYPE: Mexico, Chiapas, 15 km N of Tuxtla Gutiérrez near the cliffs of El Sumidero, 1200 m, 2 December 1951, *F. Miranda 7330* (MEXU; isotypes, F, RSA).

Distribution (Fig. 41): Locally abundant on dry, rocky slopes especially in second-growth vegetation with *Tithonia*, *Dodonaea*, *Desmodium* and *Hauya*, along the eastern and northern escarpment of the central depression of Chiapas, Mexico, and northwestern Guatemala formed by the Río Grijalva, 900–1750 m elevation. Flowering, August to March.

Additional specimens examined:

MEXICO. CHIAPAS: El Sumidero, Municipio of Tuxtla Gutiérrez, *Raven & Breedlove 19765* (leaves glabrescent), *Breedlove 14016* (both DS); Chiapa de Corzo, *Saunders 30* (US); Muctajoc, Municipio of Ixtapa, *Breedlove 7289, 13782*, *Laughlin 2101, 2291, 2294* (all DS); 5 km above Soyalo, *Breedlove 14055A* (DS); Granadía, Municipio of Zincantán, *Breedlove 7161, 7162, 7270* (all DS); 4 mi. NW of Pinola, *Raven & Breedlove 20112, 20115* (both DS); 3 mi. S of Aguacatenango, *Breedlove & Raven 13128, 13456* (both DS); 1 km N of Aguacatenango, *Breedlove 7901* (DS); without definite locality, *Ghiesbrecht 69* (GH).

GUATEMALA. HUEHUETENANGO: Pueblo Viejo Quen Santo, *Seler 2655* (GH).

As emphasized by Miranda (1962), *Lopezia langmaniae* is very distinct from *L. grandiflora*, even though Munz (1961) placed it in the synonymy of that species.

Section IV. **Lopezia**

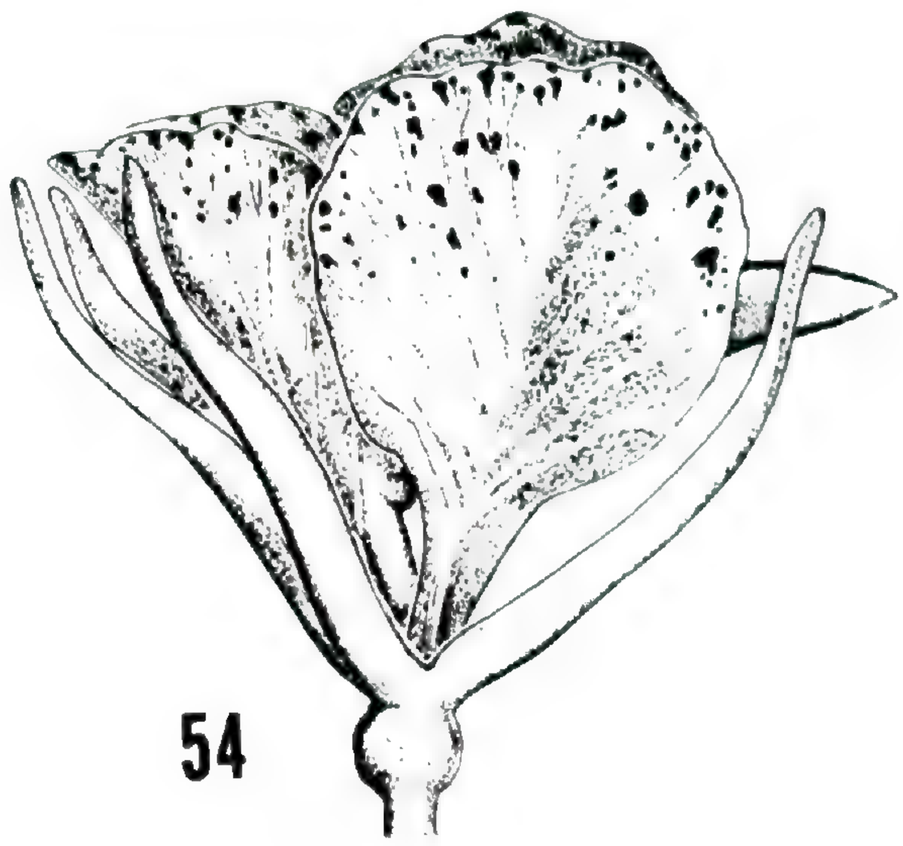
Lopezia sect. *Lopezia*

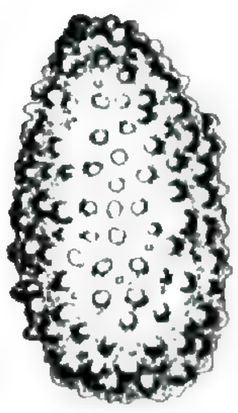
Lopezia subg. *Lopezia*; Munz, Brittonia 13: 77. 1961; N. Amer. Fl. II. 5: 17. 1965.

Annual or perennial *herbs*, rarely stoloniferous; two taxa with swollen underground parts; stems and inflorescences often reddish, the stems well branched, erect or ascending except in *L. racemosa* subsp. *moelchenensis*. *Leaves* alternate, rarely subopposite especially near the base or perhaps mainly opposite in *L. conjugens*. *Inflorescence* terminal, racemose or rarely paniculate, usually leafy. *Flowers* purplish or somewhat reddish to white, highly zygomorphic, markedly protandrous or autogamous, the parts free. *Sepals* subequal, divergent, often reddish. *Petals* clawed, the upper ones narrower than the lower ones, geniculate, with one or two glands (rarely 0) at the bend. *Upper stamen* fertile, the lower one petaloid, tightly clasping the fertile one and releasing it explosively upward at a touch, the staminode then reflexing sharply downward and the fertile stamen upward out of the circle of sepals while the style elongates and the stigma comes to occupy the same position as the dehiscing anther had previously; upper end of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. *Pollen* blue. *Capsule* subglobose or obovoid, dehiscent in upper third or at apex only in *L. trichota*, often reddish. *Seeds* many, small, ± finely tuberculate. Gametic chromosome numbers, $n = 10, 9, 8, 20$.

TYPE SPECIES: *Lopezia racemosa* Cav.

Distribution: Nearly throughout Mexico and Guatemala, mainly at middle elevations, but absent from the northern deserts and lowland tropics; one species in El Salvador, Costa Rica, and Panama at middle to high elevations.





FIGURES 53–56. *Lopezia hintonii*.—53. Inflorescence, × 0.53.—54. Flower, × 5.3.—55. Upper petal, × 4.2.—56. Seed, adaxial view, × 21. All from the holotype.

Some populations occasionally lack the snapping mechanism, but it is in general the mark of a monophyletic group with closely similar flowers. *Lopezia trichota*, with its tuberous underground parts, becomes leafless in the dry season and is one of the most distinctive species. Its capsules are nearly indehiscent and probably dispersed along streams and in flash floods.

7. **Lopezia hintonii** Foster, Contr. Gray Herb. 155: 64. 1945.—FIGS. 53–56.

Densely hirsute *perennials*. *Stems* ca. 15 dm tall, angular, appressed-hirsute. *Leaves* 1–4 cm long and 0.2–2 cm wide, ovate to lanceolate, symmetrically or asymmetrically cuneate to obtuse at base, ± acute at apex, remotely serrulate to subentire, appressed-hirsute, with hairy short petioles to 1 cm long. *Raceme* lax, with a few, slender branches; bracts 3–10 mm long and 0.5–2 mm wide, hairy toward tip; pedicels 11–23 mm long, ascending to spreading, glabrous. *Flowers* strongly protandrous. *Sepals* 6.5–9 mm long and 1–2 mm wide, subglabrous. Lower *petals* 7–9 mm long and 3.5–5.5 mm wide, broadly obovate, or more rarely ovate, tapering at base or shortly and broadly clawed, denticulate-sinuate to subentire at the rounded apex; upper petals 7.5–10 mm long and 2.5–4 mm wide, oblong-obovate, short-clawed with a winged claw, obsoletely auricled

(subhastate), biglandular below auricles, somewhat denticulate-sinuate to entire. *Fertile stamen* 7–8 mm long; anther ca. 2 mm long. *Staminode* ca. 8–9 mm long, ca. 2 mm wide, oblanceolate, narrow at the middle, acute. *Style* distinctly shorter than stamen; stigma to 1 mm in diameter. *Capsule* to at least 3.5–5.5 mm long or longer, subglobose, glabrous. *Seeds* 1–1.5 mm long, 0.5–0.7 mm thick, oblong-ovoid, slightly incurved, finely tubercled.

TYPE: Mexico, Guerrero, Mina, Yesceros-Cruz Pacifica, rocky slope in oak forest, 2550 m, 26 November 1939, *G. B. Hinton 14902* (GH; isotypes, NY, US).

Distribution (Fig. 41): Endemic in that locality. To our knowledge, no other collection has yet been made.

Unfortunately, because of the lack of recent material we have not been able to study the biology and cytology of this species. A critical feature—flower color—is unknown. Eyde and Morgan (1973) thought that it might be transitional between sect. *Jehlia* and sect. *Lopezia*, but the two glands on each upper petal seems to place it here. It seems to differ from *L. miniata* principally in its larger flowers, fruits, and seeds, and in its obscure auricles and winged claw of the upper petals.

8. **Lopezia miniata** Lag. *ex* DC., Cat. Hort. Monsp. 121. 1813. Lagasca, Gen. & Sp. Pl. Nov. 1. 1816; Munz, Brittonia 13: 80. 1961; N. Amer. Fl. II. 5: 18. 1965.

Annuals or *perennials*, sparsely to densely appressed pubescent or hirsute, with white, rusty, or reddish hairs. *Stems* 1.5–20 dm tall, pubescent or hirsute to subglabrous, subterete. *Roots* fibrous or tuberous. *Leaves* 0.7–8.5(–10) cm long and 0.15–4 cm wide, ovate or oblong-elliptic to lanceolate, obtuse, acute, or cuneate at base, acute or subacuminate at apex, serrate to subentire, hirsute, especially below, to subglabrous, sometimes with minute glandular pubescence, with (2–)4–11(–12) veins on each side of midrib; petioles (0.05–)0.1–4.5 cm long. *Inflorescence* paniculate, the terminal racemes leafy and lax or crowded; bracts 2–22 mm long and 0.5–6 mm wide; pedicels 5–35 mm long, spreading to more or less ascending-rarely suberect, puberulent, glandular-strigulose, or subglabrous. *Flowers* strongly protandrous. *Sepals* 3.5–7 mm long and ca. 1 mm wide, glabrous or with a few hairs near apex and rarely also at base. *Petals* white, pinkish, orange, or lilac; lower petals 4.5–9(–10) mm long and 1.5–5 mm wide, linear to suborbicular, long-clawed, subacute or obtuse, entire to crenulate at the apex; upper petals 4–8 mm long and 0.8–2 mm wide, linear to narrowly spatulate, the limb distinctly biauriculate near the base, with two pink or red glands below the auricles, entire, dentate, or crenulate at the apex. *Fertile stamen* 3.5–5.5 mm long; anther 1–2 mm long, gray to brownish. *Staminode* 3.5–5 mm long and 1.5–3 mm wide, obovate-spatulate, ± emarginate at apex, same color as the petals. *Style* 3–5 mm long; stigma 0.3–0.6(–0.7) mm in diameter, white or pink; ovary 1–1.5 mm thick, subglobose, subglabrous or sparsely pubescent near apex. *Capsule* 1.5–4.5(–5) mm long, 1.5–4(–5) mm thick, subglobose, subglabrous. *Seeds* 0.6–1.2 mm long, 0.5–0.6 mm thick, ovoid, finely tuberculate, brown. Gametic chromosome number, $n = 10$.

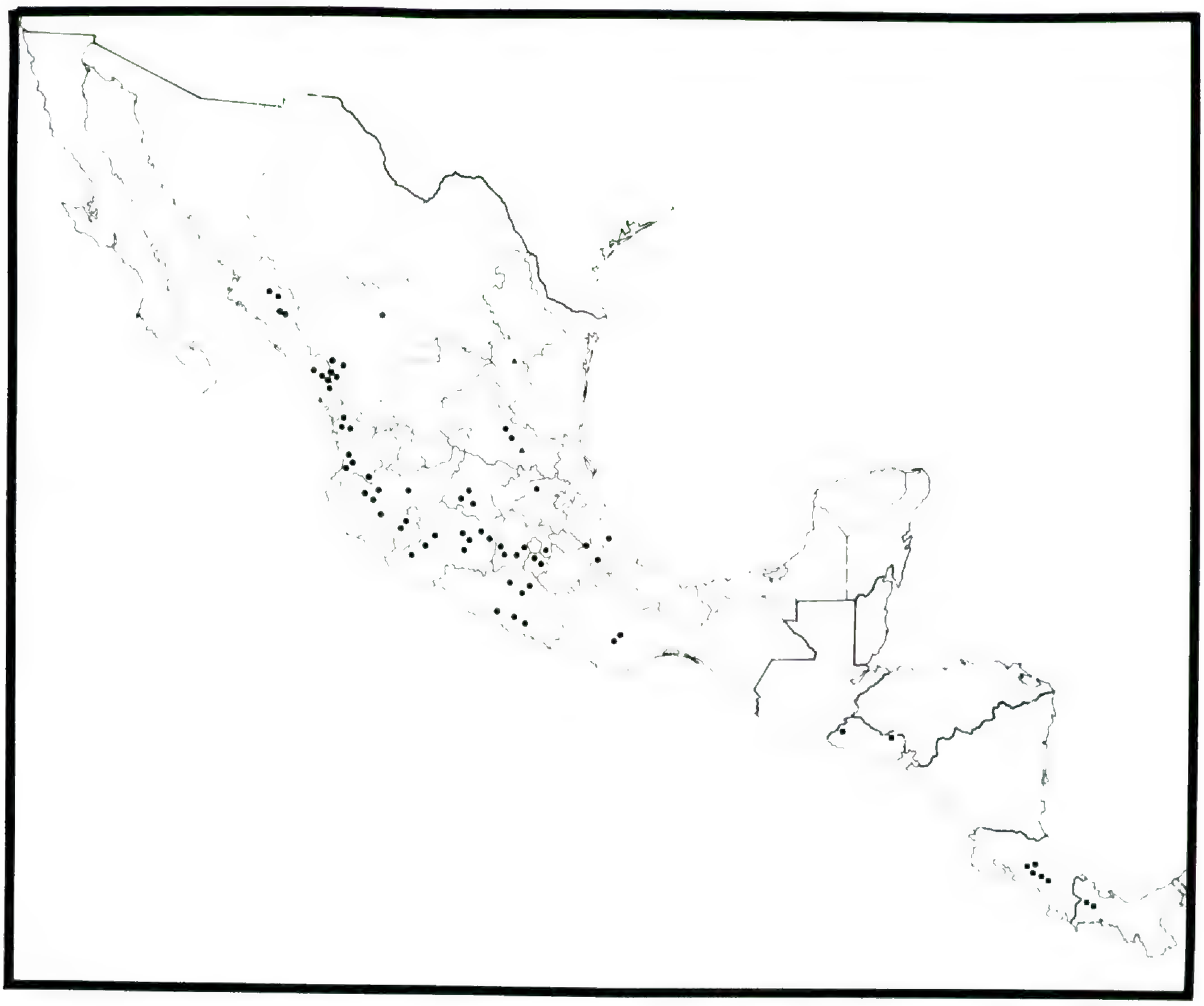


FIGURE 57. Geographic distribution of *Lopezia miniata* subsp. *miniata* (dots), *L. miniata* subsp. *paniculata* (squares), and *L. nuevo-leonis* (triangles).

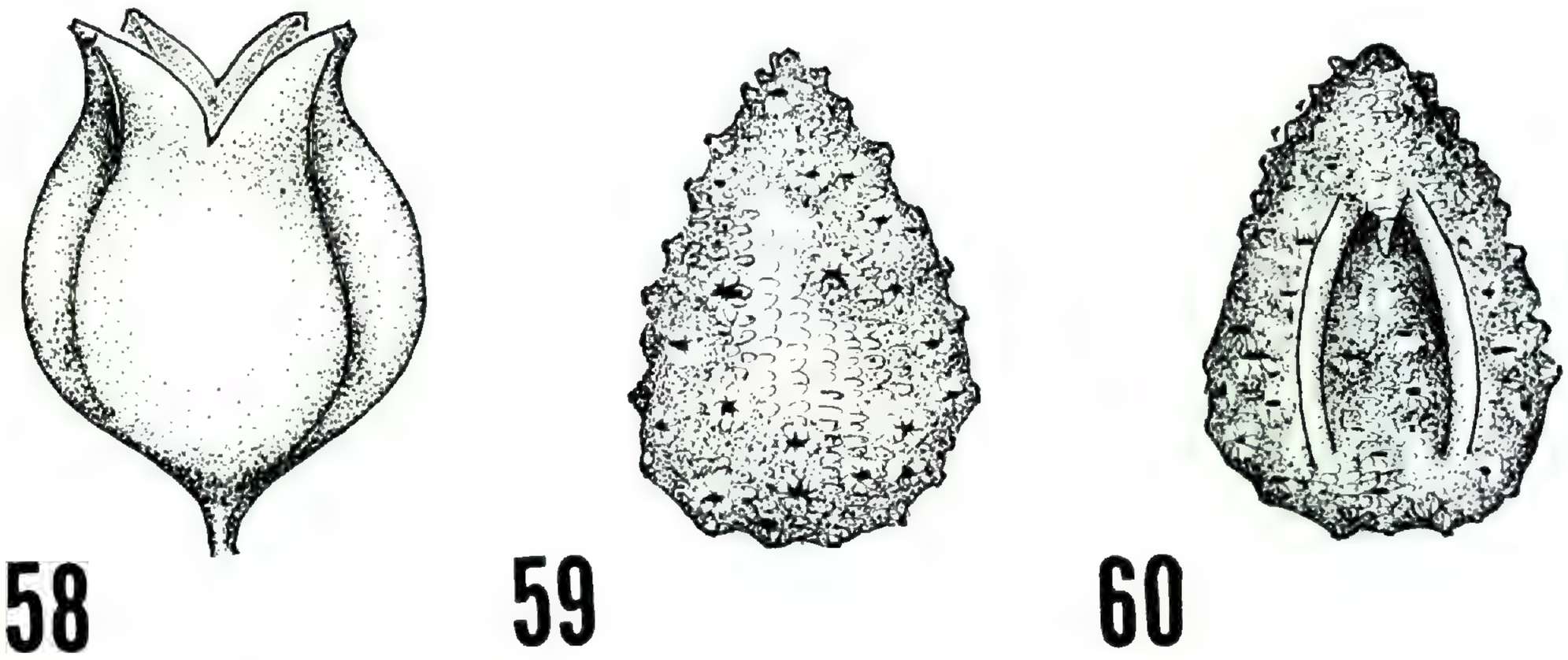
Distribution (Fig. 57): Shrubby or open situations at middle elevations, often weedy, from northern Sinaloa and Durango in the Sierra Madre Occidental south to Veracruz, Mexico; El Salvador, Costa Rica, and Panama, 700–3000 m elevation. Flowering, (August–) November to March.

The southern disjunct populations of this species have generally been regarded as a distinct species, *Lopezia paniculata* Seemann. They differ chiefly in their more crowded inflorescences and tuberous underground parts. In the experimental garden, northern and southern populations could be intercrossed without difficulty, producing fertile hybrids. The relationships between the northern populations of this species and the less variable southern ones can best be understood and demonstrated in the context of the genus, we believe, by regarding them as subspecies of a single species.

KEY TO THE SUBSPECIES

Roots fibrous; leaves and lower petals partly denticulate; racemes lax; Mexico ..... 8a. subsp. *miniata*

Roots usually tuberous; leaves and lower petals subentire; racemes usually crowded; El Salvador, Costa Rica, and Panama ..... 8a. subsp. *paniculata*



FIGURES 58–60. *Lopezia miniata* subsp. *miniata*.—58. Capsule, × 11.—59. Seed, abaxial view, × 36.—60. Seed, adaxial view, × 36.

8a. **Lopezia miniata** subsp. **miniata**.—FIGS. 58–60.

Lopezia frutescens Roem. & Schult., Syst. 1: 34. 1817. Type: BM, herb. Roemer, "habit in Mexico"; cultivated (?) in W.

Lopezia pumila Bonpl., Desc. Jard. Malm. 1813: 67. 1815. Type: Mexico, Guanajuato, near Guanajuato, *A. Bonpland* (P, herb. Bonpland, lectotype).

Lopezia fruticosa Hort. Par. *ex* Schrank, Nov. Act. Nat. Cur. 9: 91. 1818, and Pl. Rar. Hort. Acad. Monac. 1: *fol.20*. 1818/19. Type: Portenphlag Herbarium and cultivated in W probably from the authentic material; Hort. bot. Monac., herb. Zuccarini, "*L. fruticosa* Schrank, h. in Mexico" 1820 (M, cultivated from the authentic?).

Lopezia pubescens HBK., Nov. Gen. & Sp. 6: 96. 1823. Type: Mexico, Michoacán, Patzcuaro, 6780 ft., *A. von Humboldt & A. Bonpland* (P).

Lopezia oaxacana Rose, Contr. U. S. Natl. Herb. 12: 229, *fig. 42*. 1909. Type: Mexico, Oaxaca, San Felipe, 10 October 1897, *C. Conzatti & V. González 509* (US 574,851; isotype, GH).

Lopezia palmeri Rose, Contr. U. S. Natl. Herb. 12: 299, *fig. 43*. 1909. Type: Mexico, Durango, San Ramón, 21 April–18 May 1906, *E. Palmer 85* (US 571,100; isotypes, GH, K, MO, NY, S, UC).

Lopezia violacea Rose, Contr. U. S. Natl. Herb. 12: 301, *fig. 48*. 1909. Type: Mexico, Morelos, Sierra de Tepoxtlán, 2350 m, 30 October 1900, *C. G. Pringle 8358* (US 381,869; isotypes, BM, DS, G, GH, MEXU, MO, NY, POM, UC, W, Z).

Lopezia stricta Rose, Contr. U. S. Natl. Herb. 12: 301, *fig. 47*. 1909. Type: Mexico, Jalisco, Sierra Madre W of Bolaños, 15–17 September 1897, *J. N. Rose 2979* (US 301,735; isotypes, GH, NY).

Lopezia pauciflora Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Mexico, Sierra Madre Occidental, *B. C. Seemann 2169 partim* (K).

Lopezia tepicana Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Mexico, Nayarit, Tepic, *Sinclair* (K).

Lopezia globosa M. E. Jones, Contr. West. Bot. 15: 147. 1929. Type: Mexico, Nayarit, Tepic, *M. E. Jones 23299* (POM).

Annuals or *perennials*, sparsely to densely appressed-pubescent or hirsute, with white, rusty, or reddish hairs. *Leaves* serrate to subentire. *Inflorescence* leafy and rather lax. *Petals* white, pinkish, orange, or lilac; lower petals (4.5–) 4–9(–10) mm long and 2–5 mm wide, denticulate or crenulate to subentire at the apex; upper petals 5–8 mm long and 0.8–2 mm wide. *Seeds* 0.6–1(–1.2) mm long. Gametic chromosome number, $n = 10$.

TYPE: Cultivated at Montpellier, France, the seeds sent from Mexico by Martin Sessé y Lacasta, 1804, *A. P. De Candolle* (G-DC; probable isotype, US). Possibly the same material used for the illustration of *Enthomanthus fibrosus* by Mociño and Sessé.

Distribution (Fig. 57): Mexico, almost ubiquitous in pine-oak vegetation but also very common as a roadside weed and as a weed in *milpas* from northern Sinaloa and Durango, south through the Sierra Madre Occidental to central Oaxaca and across the Tarns-Mexican Volcanic Belt to Veracruz with a few scattered localities in Hidalgo and San Luis Potosí, 700–3000 m elevation. Flowering, (August–) November to March.

Representative specimens examined:

MEXICO. SINALOA: Balboa, San Ignacio, *Ortega 1152* (DS, MEXU); Cerro de la Silla, San Ignacio, *Móntez & Salazar 734* (US); Santa Lucía, Concordia, *Ortega 6035* (IPN); 19 mi. E of Concordia on Mex. Hwy. 40, *Breedlove 1621* (DS, RSA); 45 mi. E of Concordia, *Breedlove 4249* (DS); Capadero, Sierra Tacuichamoma, *Gentry 5536* (DS, GH, MEXU, MICH, MO, NY, UC, US); Ocurahui, Sierra Surutato, *Gentry 6423* (MICH); Canon Tarahumare at La Joya, Sierra Surutato, *Breedlove 15608* (DS); 4 mi. W of Surutato, Sierra Surutato, *Breedlove 15598* (DS). DURANGO: La Bajada, Tamazula, *Ortega 595* (DS, IPN, MEXU), *4265* (US); Sianori, *Ortega 5361* (US, K); Sierra Tres Picos, *Gentry 5297* (DS, GH, MEXU, MICH, MO, NY, UC, US); 19 mi. SW of San Ramón, *Palmer 85*; 13 mi. W of La Ciudad, *Breedlove 15549* (DS); 9.3 mi. E of El Palmito, Pueblo Nuevo, *Breedlove 4256* (DS). NAYARIT: Tepic, *Palmer 1893* (DS, GH, MICH, S, UC, US), *Jones 23189* (POM); N of Compóstela, *McVaugh & Koelz 513* (MEXU, MICH, RSA, US); vicinity of Jalisco, *Ferris 5825* (A, DS, US); 10 mi. SE of Ahuacatlán, road to Barranca del Oro and Amatlán, *McVaugh & Koelz 802* (MICH); W side of Cerro de Sanganguëy, *Breedlove 8053*, *Breedlove & Gregory 14218* (both DS). SAN LUIS POTOSÍ: "Sangudo," *Schaffner 640* (GH, K; NY, pro parte); Sierra de Álvarez, around Puerto Huerta, Zaragoza, *Rzedowski 4184* (IPN); Cerro Grande, NW of Guadalcazar, *Rzedowski 5067* (RSA); exact locality not known, *Schaffner 443* (BM, G, MICH, NY, P, UC). GUANAJUATO: Ravín de "la Esperanza," 6 km from Guanajuato, 1893, *Dugés* (GH); León, *Rose & Rose 11508* (NY, US); Ojo de Agua, S of Abásolo, *Sohns 243* (US). HIDALGO: 20 km NE of Zimapan, *González Quintero*, 1965 (with a few features of *L. racemosa*, e.g. scarcely auricled petals; DS). JALISCO: Sierra de Manantlán, SE of Autlán, *McVaugh 23099* (hairy form with large petals; IPN, MICH), *Hooper*, 1953 (MICH); La Barranca, Guadalajara, *Jones 27077* (a delicate many-stemmed form with lilac narrow petals; BM, DS, MICH, MO, NY, RSA, UC, US); Sierra de la Campana, W of Los Volcanes, *McVaugh 20026* (MICH); Etzatlán road to San Domingo mines, *Barnes & Land 298* (K, US), *Rose & Painter 7514* (US), *Pringle 11454* (DS, GH, MEXU, MICH, MO, UC, US); Sierra del Tigre, S of Mazamitla, *McVaugh & Koelz 427* (MICH, RSA); Sierra del Halo, *McVaugh & Koelz 1251* (MICH); Sierra de Cuale, SW of Talpa de Allende, *McVaugh 14377* (MEXU, MICH, RSA, US), *14259* (MEXU, MICH, RSA); 12 mi. W of Autlán on Mex. Hwy. 80, *Breedlove 8069* (DS); 11 mi. W of Tecalitlán, on Mex. Hwy. 110, *Breedlove 8072* (DS); Barranca W of Atenquique, Tuxpán, *Rzedowski 21934* (IPN). MICHOACÁN: Near San Lorenzo, N of Uruapán, *Frye & Frye 3056* (DS, GH, POM, UC); 3 km S of Tacambaro, on road to Pedernales, *Rzedwoski 23724* (DS, IPN); ca. 17 mi. E of Morelia, *Breedlove 7228A* (DS); 5 mi. S of Zinapecuaro, *Breedlove 7217* (DS); Morelia, Cerro Azul, *Arsène 2830* (BM, K, MO, NY, US); Sierra Torrecillas, Coalcomán, *Hinton et al. 12337* (G, GH, K, MICH, NY, P, S, UC, US, W), *15264* (US 1,977,671; sheets in other herbaria are *L. racemosa*); Patzcuaro, *Pringle 3953* (BM, DS, G, GH, IPN, K, M, MEXU, MO, NY, P, POM, S, UC, US, W, Z); W of Jacona, *Ripley & Barneby 14067* (NY). GUERRERO: Pie de la Cuesta Toro Muerto, dist. Galeana, *Hinton 11075* (unique tall form with large flowers, leaves and panicles; G, GH, K, M, MICH, MO, NY, S, UC, US, W); Sierra Madre del Sur, N of Río Balsas, *Mexia 8786* (G, GH, MO, NY, RSA, S, UC, US); Plan del Carrizo, *Hinton et al. 11026* (GH, K, MICH, NY, UC, US); above Los Ranchos, W of Teloloapán, *Porter 1357* (DS, GH, MEXU); 2 mi. NW of Filo del Caballo, *Breedlove 15826* (DS); 2 mi. E of Omiltemi, *Breedlove 15817* (DS); Mountains SW of Taxco, *Ripley & Barneby 13725* (DS). MEXICO: Tultenango, *Rose & Painter 7824* (GH, NY, US); Rincón, Temascaltepec, *Hinton et al. 6792* (G, GH, K, MICH, NY, S, UC, US, W), *Hinton 209* (MEXU); Tejupilco, Temascaltepec, *Hinton et al. 7327* (GH,

K, NY, US); Ozumba, *Pringle 8713* (BM, G, GH, IPN, K, M, MEXU, MICH, NY, P, RSA, TEX, UC, US, W), *9797* (GH, MO, NY, US, Z); Cerro Ajusco, *Mexia*, 1922 (UC); Jilotepec, *Matuda et al. 26724* (MEXU); Valle Bravo-Ixtapantango, *Miranda 4797* (MEXU); 15 mi. E of Zitacuaro on Mex. Hwy. 15, *Breedlove 8074* (DS); Coatepec Harinas, *Ripley & Barneby 13759* (DS). MORELOS: Casa del Tepozteco, *Seler 4328* (GH); Sierra de Tepoxtlán, *Pringle 8357 p.p.* (G, IPN, MEXU, NY, US, Z); S of the village of Tepoztlán, *Ripley & Barneby 14549* (DS); Amatlán, *Miranda 918* (MEXU); 3 mi. S of Tres Cumbres, *Breedlove & Gregory 14232* (DS). PUEBLA: Cerro Sta. Maria de Zacatepec, *Arsène 3511* (MO, NY, P, US). VERACRUZ: Near El Puerto, above Acultzingo, *Sharp 44659* (RSA); near Jalapa, *Pringle 9230* (TEX, UC). OAXACA: Sierra de San Felipe, *Ch. L. Smith 844 p.p.* (leaves, flowers and capsules larger than usual; MO, US); Santa Cruz, Orillas del San Antonio, *Conzatti et al. 4097* (US); Oaxaca, *Conzatti & Gonzales 1055 p.p.* (GH), *Ghiesbreght 261*? (P); Las Sedas, *Conzatti 2030* (BM, MEXU).

Lopezia miniata subsp. *miniata* is highly variable and polymorphic. Its variation is parallel to that of *L. racemosa* subsp. *racemosa* (*e.g.* in color of petals). Both taxa are widely distributed in Mexico, growing sympatrically in many localities and occupying almost the same habitats. In spite of the overall similarity between the two, a detailed examination shows that *L. miniata* subsp. *miniata* is well defined by an assemblage of characters: leaves never distinctly serrate; petals never oblong; claws of petals never ciliolate; lower petals denticulate or subentire, upper petals truncate-obtuse to usually slightly retuse or few-denticulate, distinctly biauriculate and with 2 obvious glands; stigma minute; capsules small. It flowers mainly in the dry season (November–March) whereas *L. racemosa* flowers mainly in the wet season (June–October).

The variability of *Lopezia miniata* subsp. *miniata* is particularly pronounced in:

1. *Habit*: Perennials *vs.* annuals, the latter sometimes differing considerably from the more common perennials; the perennials flower in their first year. Unusual forms are more common among the annuals. Stems may be few or many, simple (*e.g.* "*L. pumila*") or branched, short or very long, ascending, erect, or decumbent.

2. *Pubescence*: From densely hirsute or pubescent (*e.g.* "*L. pubescens*") to subglabrous. The variation occurs between and within populations as well as on individual plants. The hairs may be of different kinds and positions, spreading to usually appressed, and in different proportions. The various parts are almost independently variable in this character, though hairy bracts and buds have not been found in glabrescent plants. Only hairy specimens have been recorded from the east (Hidalgo, Puebla, Veracruz).

3. *Leaf*: Wide range of variation in dimensions and general morphology. Of all organs the leaves show the most age- and season-related variablity.

4. *Petals*: Variable in size (*e.g. Espinosa 103* from Morelos with small flowers *vs. Hinton 5343* from Mexico with long petals) and color. Two divergent types have been observed: Corolla with the dominant color white, tinged with pink, lilac, blue or even violet (*e.g.* "*L. violacea*") as distinct from corolla pink-reddish or orange to red. The first form has usually smaller capsules and flowers, upper petals truncate to retuse-denticulate and lower petals denticulate; the second form is sometimes long-stemmed, with larger flowers, particularly petals, usually with bigger capsules, the upper petals somewhat retuse and the lower ± retuse but subentire. The "whitish-flowered" type is distributed mainly in the

north (Sinaloa, Durango, Nayarit south to México) and very scattered in the south (Guerrero); the "reddish-flowered" type occurs mainly in south and central Mexico, from Nayarit and San Luis Potosí to Oaxaca. The "whitish-flowered" type is better represented in herbaria, probably because more specimens have been collected in northern Mexico. Nevertheless, it seems that the "reddish-flowered" form is as common as the other one and more widespread; it is less weedy, growing chiefly in primary habitats. We did not keep these two forms apart, as distinct subspecies, for several reasons: they are easily crossed; the morphological differences are not clear-cut as all characters show a ± continuous variation, except for the color which in itself is not considered a useful character upon which to delimit subspecies; they are not separate eco-geographically.

5. *Glands and auricles*: The glands are variable in size, color and position, but the range of variation is rather narrow. They may be close together or apart, equal or rarely one smaller. More variable are the auricles which can be short or long, wide or usually narrow, spreading straight to bent upwards.

6. *Capsules*: Generally smaller than those of *L. racemosa* but sometimes to 5 mm in diameter. There is also some variation in the number of fruits (or flowers, *e.g.* "*L. pauciflora*") per plant, though commonly the inflorescence is many-branched and many-fruited.

The various mentioned characters are uncorrelated (*e.g.* pubescent plants may have whitish or reddish flowers, smaller or larger capsules, and are not restricted to certain localities). For this reason the species has a complex synonymy. It is preferable to treat this taxon as one polymorphic entity, following Munz (1961), instead of recognizing in it a multitude of ill-defined subdivisions.

A few extreme forms of *Lopezia miniata* should be noted explicitly:

a). Plants with short, nodding and bowed pedicels; flowers small; upper petals with short but broad auricles and 2 adjacent glands; capsule wide (± 3.5 mm). Mexico, Michoacán: Cerro Azul, near Morelia, 4 November 1909, *Arsène* (NY). This is so far one of the very few plants collected which share a few features with *L. racemosa* (others are *Conzatti & Gonzalez 509* from Oaxaca and *González Q.*, 1965, from Hidalgo). No other natural hybrids or transitions between the two species have been found, though in many respects (stature, pubescence, dimensions of flowers and capsules) they show homologous, almost parallel, variability. This phenomenon accounts for many misidentifications of both, especially in herbarium material.

b). Plants with long stems and large leaves; flowers and capsules larger than usual; glands minute; but (sepals) with few long hairs at base and tip. Mexico, Oaxaca, San Felipe, 10 October 1897, *Conzatti & González 509* (GH, US; type collection of *L. oaxacana* Rose); Sierra de San Felipe, 2 October 1894, *C. L. Smith 844 pro parte* (MO, US; paratypes of *L. oaxacana*).

c). Plants with long stems, glabrescent; leaves large (to 9 cm long and 5 cm wide); racemes ± paniculate; ovary and bud long-ciliate. Mexico, Veracruz near El Puerto, above Acutzingo, 6 September 1944, *Sharp 44659* (RSA).

d). Plants with hirsute and hispid-pubescent stems; some leaves subopposite; pedicels glandular-puberulent to pubescent; petals large, the upper ones oblanceolate to oblong; fertile stamen long (5–6 mm). Mexico, Jalisco, Sierra de

Manantlán, SE of Autlán, between El Chante and Cuzalapa, 19–22 March 1965, *R. McVaugh 23099* (IPN, MICH).

e). Tall (to 3 m?), pubescent plants; leaves long (to 11 cm), the upper subopposite; inflorescence long, branched, many-panicled; stipules acicular-subulate; bracts and buds ± hirsute; all floral parts longer than usual; corolla orange; capsule 0.3–0.55 mm; seeds ca. 1.1 mm long, brown-red. Mexico, Guerrero, Dist. Galeana, Pie de la Cuesta Toro Muerto, 17 December 1937, *G. B. Hinton 11075* (G, GH, K, MICH, MO, NY, S, UC, US, W). Probably an undescribed taxon, related to *L. miniata* but quantitatively distinguished. This collection seems to approach the type of *L. hintonii* in its characteristics.

f). Delicate plants with many thin stems, hirsute-pubescent to glabrescent; leaves narrower than usual, subentire; inflorescence paniculate, many flowered; pedicels slender, glandular-puberulent; flowers (in herb.) lilac-violet; petals narrow, long clawed; seeds finely tubercled. Mexico, Jalisco, Guadalajara, La Barranca, 17 November 1930, *M. E. Jones 27077* (BM, DS, MICH, MO, NY, RSA, UC, US). Probably an undescribed taxon, closely related to *L. miniata*.

8b. **Lopezia miniata** subsp. **paniculata** (Seemann) Plitmann, Raven & Breedlove, comb. nov.

Lopezia paniculata Seemann, Bot. Voy. Herald 120. 1853. Munz, Brittonia 13: 82. 1961; N. Amer. Fl. II. 5: 19. 1965.

Densely hirsute *perennials*. *Leaves* remotely serrulate to subentire. *Inflorescence* usually of short and crowded terminal racemes. *Petals* white or reddish-pink; lower petals 5–7 mm long and 1.5–3 mm wide, somewhat retuse or subentire at the apex; upper petals 4–7 mm long, ca. 1 mm wide. *Seeds* ca. 1.2 mm long. Gametic chromosome number, $n = 10$.

Type: Panama, Boquete, March 1848, *B. C. Seemann 1225* (K; isotype, BM).

Distribution: Moist or dry places such as slopes, canyons and even roadsides, in shrubby or open formations in El Salvador, Costa Rica and Panama, (850–)950–2000(–2600) m elevation. Flowering mainly from November to March, but sporadically throughout the year.

Representative specimens examined:

El Salvador. morazon: Montes de Cacaquatique, *Tucker 663* (MICH, RSA, UC, US). ahuachapan: Apaneca, *Pittier 2010* (racemes rather long, upper leaves and bracts subglabrous; US).

Costa Rica. alajuela: Cerros de San Rafael de San Ramón, *Brenes 5905* (CR, NY), *5923a* (CR), *21999* (NY). san josé: Cerro de Piedra Blanca, above Escasú, *Standley 32555, 35776, 41381* (all US); Paraíso, *J. D. Smith 6503* (US); Río Blanco, NE of El Copey, *Standley 41909* (US). cartago: San Cristóbal de Candelaria, *Pittier 3679* (NY, US); Cerro de la Carpintera, *Standley 34210* (US); Volcán de Irazú, *Holway 282* (POM, US).

Panama. chiriquí: El Boquete, *Killip 3505* (US), *Pittier 2890* (NY, US); Cerro Punta near El Volcán, Río Chiriquí Viejo valley, *G. White 30* (GH, MO); Volcán de Chiriquí Viejo, *Allen 987* (G, GH, MO, US); Bajo Mono, district Boquete, *Davidson 493* (MO, US).

Lopezia miniata subsp. *paniculata* is variable in stature (height), pubescence, dimensions of leaves and racemes, and to a lesser extent in flower-color, length of raceme and size of capsule. Nevertheless, it is much less variable than the northern, widespread subsp. *miniata*, from which it has almost certainly been

derived. Plants of subsp. *paniculata* with elongated, loose and leafy racemes have been collected occasionally (*Davidson 493* from Panama; *Pittier 2010* from El Salvador; *J. León 2207* and *Smith 6503* from Costa Rica). It is not certain how constant the tuberous underground parts may be in this subspecies, as they are rather infrequently collected.

9. **Lopezia suffrutescens** Munz, Brittonia 13: 80. 1961. Munz, N. Amer. Fl. II. 5: 18. 1965.—FIGS. 61–62.

Robust, bushy, subglabrous, fleshy *perennials*. *Stems* 4–8 dm tall, thick, juicy, well branched; branches ± angular, subglabrous but sparsely hirtellous near the inflorescence. *Leaves* 1–7.3 cm long and 0.3–4 cm wide, thick and ± fleshy, ovate or lanceolate, obtuse and sometimes asymmetrical at base, acute or acuminate at apex, acutely serrate or serrulate, with 3–9 veins on each side of midrib, ciliolate along margins and veins; petioles 0.15–2.5 cm long, narrowly winged, sparsely hispidulous. *Bracts* 5–42 mm long, 1.5–11 mm wide, glabrous; pedicels ascending to recurved-spreading, to 3.5 cm long. *Flowers* strongly protandrous, evidently nectariferous. *Sepals* 6–14 mm long and 1–2 mm wide, subglabrous but with a few erect hairs near tip and base. *Petals* pale pink or white; lower petals (7–)8–14 mm long and (3–)5–9.5 mm wide, obovate or spatulate to subdeltoid, tapering into a long claw, rounded and subentire or somewhat crenulate at apex; upper petals more deeply lined with pink, (7–)8–14 mm long and 2–7 mm wide, spatulate or oblong-oblanceolate, obtuse and subentire or somewhat crenulate at apex, narrowed then broadly auriculate at base, the auricles 1–2.2 mm high, subtended by 2 green glands on each petal, the petals subsessile. *Fertile stamen* 6–11 mm long, reddish. *Staminode* 5–10 mm long and 2.5–4 mm wide, petaloid, obovate-spatulate and ± emarginate to obcordate, white or pale pink. *Style* 6–12 mm long, pale pink; stigma 0.6–1 mm in diameter; ovary subglobose, glabrous. *Capsule* 3–5 mm thick, subglobose, glabrous. *Seeds* 1–1.5 mm long, 0.3–0.5 mm thick, oblong-ovoid, tuberculate, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Durango, La Bajada, Tamazula, 1921, *J. G. Ortega 4264* (US; isotypes, IPN, MEXU, POM, US), *567* (MEXU, probably part of the type collection).

Distribution (Fig. 41): Known only from two steep-walled canyons in Sinaloa and Durango, Mexico, 1200–1500 m elevation. Flowering February and March. *Lopezia ciliatula* is restricted to the same two areas, as far as known.

Additional specimens examined:

MEXICO. SINALOA: Cañon de Tarahumare, Sierra Surutato, *Gentry 7302* (GH, MICH, NY). DURANGO: Río Tamazula between La Bajada and La Junta, ca. 1500 m, *Breedlove 24534* (CAS).

As Munz (1961: 88) pointed out, *Lopezia suffrutescens* is amply distinct among the bituberculate species. It is very attractive, with its large pale flowers.

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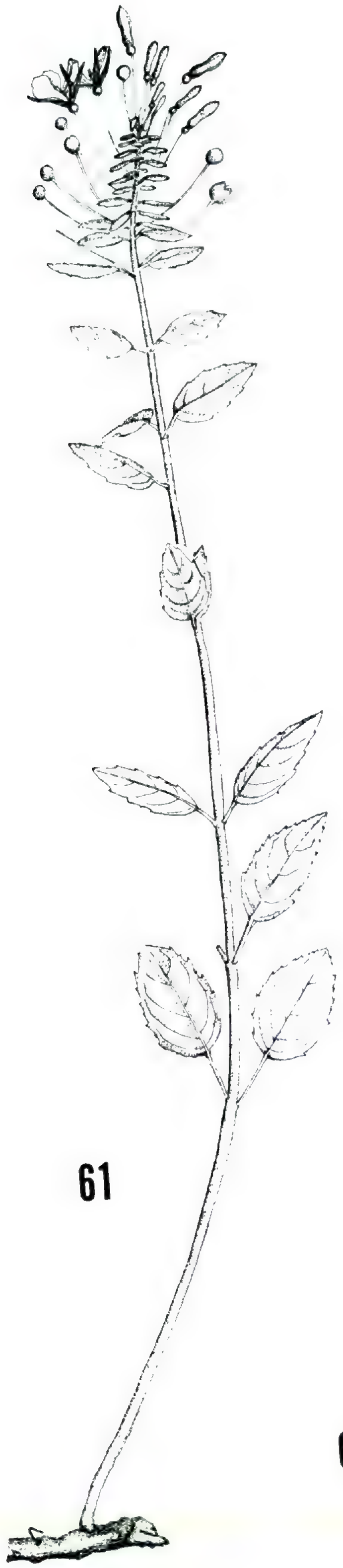
FIGURES 61–62. *Lopezia suffrutescens*.—61. Branch, × 0.6.—62. Upper petal, × 2.4. Both from the holotype.


61
62

Judging from its reduced chromosome number, $n = 9$, it was probably derived from large-flowered ancestors with $n = 10$, perhaps resembling *L. hintonii* or the population of *L. miniata* from Guerrero described on p. 523.

10. **Lopezia nuevo-leonis** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 280. 1973.—Figs. 63–65.

Sparsely strigulose to glabrous *annuals* or *perennials*. *Stems* 2.5–7 dm tall, angular. *Leaves* 0.6–4 cm long and 0.2–2.5 cm wide, oblong-ovate to lanceolate, rounded to broadly cuneate at base, subacute or acuminate at apex, acutely serrate, ± fleshy, subglabrous, with 2–6 veins on each side of midrib; petioles 0.1–3.8 cm long, scarcely strigulose or glabrous. *Bracts* 3–13 mm long and 1–4 mm wide, subglabrous; pedicels 8–21 mm long, ascending, appressed and shortly pubescent on one side, subglabrous on the other. *Flowers* mainly autogamous. *Sepals* 4.5–7 mm long and 1 mm wide, glabrous. *Petals* pink and reddish; lower petals 5–8 mm long and 2–3.5 mm wide, obovate, somewhat asymmetrically angustate into a long claw, rounded at apex, sometimes subcrenulate or slightly retuse; upper petals 5–8.5 mm long and 1–1.5 mm wide, narrowly oblanceolate, ± obtuse, clawed, shortly and obtusely auricled with 2 adjacent pink glands on each one. *Fertile stamen* 4–5 mm long; anther 1.5–2 mm long, bluish-gray. *Staminode* 3.5–4.5 mm long and 2–3 mm wide, broadly obovate, ultimately shedding pollen directly on the stigma, abruptly clawed, emarginate at apex, pink-reddish but whiter below. *Style* 3–4 mm long; stigma 0.5–1.1 mm in diameter; ovary mostly glabrous but shortly pubescent below, subglobose. *Capsule* 3–5 mm long, 2–4 mm thick, oblong or ovoid-ellipsoid, subglabrous. *Seeds* 0.9–1.1 mm long, 0.6–0.8 mm thick, oblong-ovoid, slightly incurved, coarsely rugose-tubercled, blackish. Gametic chromosome number, $n = 8$.

Type: Mexico, Nuevo León, Sierra Madre Oriental, Santa Rosa Canyon, 21 mi. W of Linares, cool N-facing talus and rock ledges, 2100 ft. elevation, 28 October 1964, *H. D. Ripley & R. C. Barneby 13569* (DS; isotype, NY).

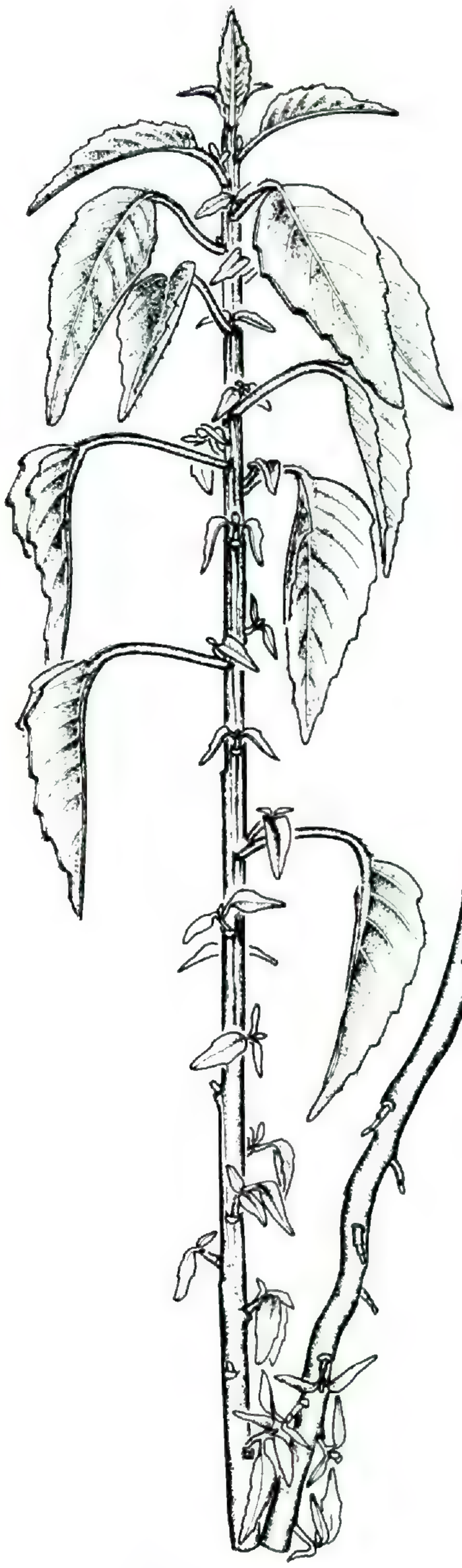
Distribution (Fig. 57): Rare and local on rocky slopes in Sierra Madre Oriental in Nuevo León and San Luis Potosí, Mexico, ca. 600 m elevation. Flowering, October and November.

Additional specimen examined:

Mexico. san luis potosí: En route from San Luis Potosí to Tampico, *Palmer 256 1/2* (BM, MO, NY, POM, S, US).—Most of these specimens include elements of *L. racemosa*. The specimens at BM, MO, POM, and S list the collectors as Parry and Palmer; however, McVaugh (1956: 308) clearly states that Parry had already departed at this time in Palmer's trip.

Lopezia nuevo-leonis occurs at the margins of the range of the genus, and only two populations are known, one from Nuevo León, the other from San Luis Potosí. Both populations are restricted to the Sierra Madre Oriental and in spite of their geographical separation—which may only be apparent since the rugged country between them has seldom been visited by botanists—they are quite similar in morphology.

Lopezia nuevo-leonis is distinguished from the related *L. miniata* by its angular reddish stems; acutely serrate leaves (generally glabrous, fleshy and with fewer veins); pink-reddish flowers; shortly and obtusely auricled upper petals;



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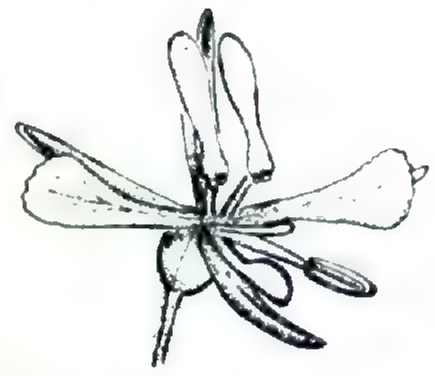

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65

FIGURES 63–65. *Lopezia nuevo-leonis*.—63. Branch, × 1.2.—64. Flower, × 2.3.—65. Seed, abaxial view, × 23. All from progeny of the holotype, grown at Stanford University.

oblong or ovoid-ellipsoid and somewhat longer capsules; coarsely rugose-tubercled, blackish and slightly larger seeds. In many of these features, including its reduced chromosome number, it resembles *L. suffrutescens*, an equally restricted endemic of the Sierra Madre Occidental. Because of its chromosome number ($n = 8$) and ecology, we assume that *L. nuevo-leonis* has been derived from populations similar to *L. miniata* as a marginal, ecologically and geographically separated population adapted to more xeric environments.

11. **Lopezia cornuta** S. Wats., Proc. Amer. Acad. Arts 21: 429. 1888. Munz, Brittonia 13: 49. 1961; N. Amer. Fl. II. 5: 18. 1965.

Annual *herbs*, ± hirsute, especially at base, or subglabrous. *Stems* 1.5–5.5 dm tall, angular. *Leaves* 0.9–4.5 cm long and 0.2–2.4 cm wide, ovate to narrowly lanceolate, rounded or cuneate at base, acute to acuminate at apex, subentire, subglabrous, sparsely ciliate or ciliolate at margins, with 2–7 veins on each side of midrib; petioles (0.1–)0.2–1.2(–2) cm long, hirsute or subglabrous. *Pedicels* 10–30 mm long, ascending, drooping in fruit, ± hairy. *Sepals* 4–7 mm long and 1–1.5 mm wide, glabrous. *Lower petals* 0.4–9 mm long and 3–6 mm wide, obovate-spatulate, clawed, rounded or subacute at apex, somewhat crenulate, red-streaked in the middle, the rest pink-red; upper petals 4–6 mm long and ca. 1 mm wide, linear-oblong, shortly clawed, somewhat dilated-auricled at base of limb, obtuse, each with two green glands just above claw. *Fertile stamen* 3–4.5 mm long; filament ca. 2.5 cm long; anther ca. 1.5 mm long, whitish. *Staminode* 3–5 mm long, obovate-spatulate, angustate at base, retuse at apex, whitish. *Style* 2–4 mm long; stigma ca. 0.5 mm in diameter, pinkish; ovary obconical-obovoid, longer than wide, angular. *Capsule* (2.5–)3.5–7 mm long, 3–5 mm thick, obovoid-obconical, angular, truncate but horned just below the apex; valves wrinkled-tubercled, separating only slightly, each ending as a broad triangular bent tooth. *Seeds* one or several in each locule, 0.1–2 mm long, ca. 1 mm thick, ovoid, wrinkled and grossly tubercled, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Chihuahua, Cumbre, October 1885, *E. Palmer 367* (GH, lectotype, Munz, Brittonia 13: 80. 1961; isotypes, BM, MEXU, NY, US).

Distribution (Fig. 66): Known only from local populations on moist ledges in pine-oak forests lining the steep barrancas of Sonora, Chihuahua, Sinaloa and Durango, Sierra Madre Occidental, Mexico, 2100–3000 m elevation. Flowering, September to November.

Additional specimens examined:

MEXICO. SONORA: La Mesa Colorada, *Gentry 521* (DS), *521M* (MICH). DURANGO: 13 mi. W of La Ciudad, *Breedlove 15547* (DS); Sandía, *Pringle 10103* (BM, DS, G, GH, IPN, K, M, MEXU, MICH, MO, NY, P, S, UC, US, W, Z); El Salto, *Maysilles 7837* (RSA); NE of El Paraíso, between Villa Union and El Salto, *Ownbey 1955* (BM, MICH, NY, S, UC, US); San Luis del Río, *Breedlove 18830* (CAS). SINALOA: 5 mi. NE of La Cienega, Sierra Surutato, *Breedlove & Kawahara 17050* (CAS); Bufa de Surutato, 3 mi. SE of Los Hornos, *Breedlove & Thorne 18452* (CAS, RSA).

Two groups of populations are recognized in *Lopezia cornuta*. Northern populations (Chihuahua, Sinaloa and Sonora), growing in pine and oak forests, consist of plants that are smaller in all respects than the southern ones (Durango), growing in barrancas and canyons, which are more lush. Accordingly, the whole species displays quantitative variation in length of stems, size of leaves and dimensions of flowers and capsules. The variation is continuous (or overlapping) and the two populations are not divergent enough (contrary to the similar situation in *L. laciniata*) to be recognized as subspecies.

The type of *Lopezia cornuta* belongs to the northern group (with stems to 30 cm; leaves to 3.2 cm long and 1 cm wide; flowers to 5.5 mm long; capsules to 4 mm long). The type locality is the same as that of *L. gracilis*. Vegetatively the

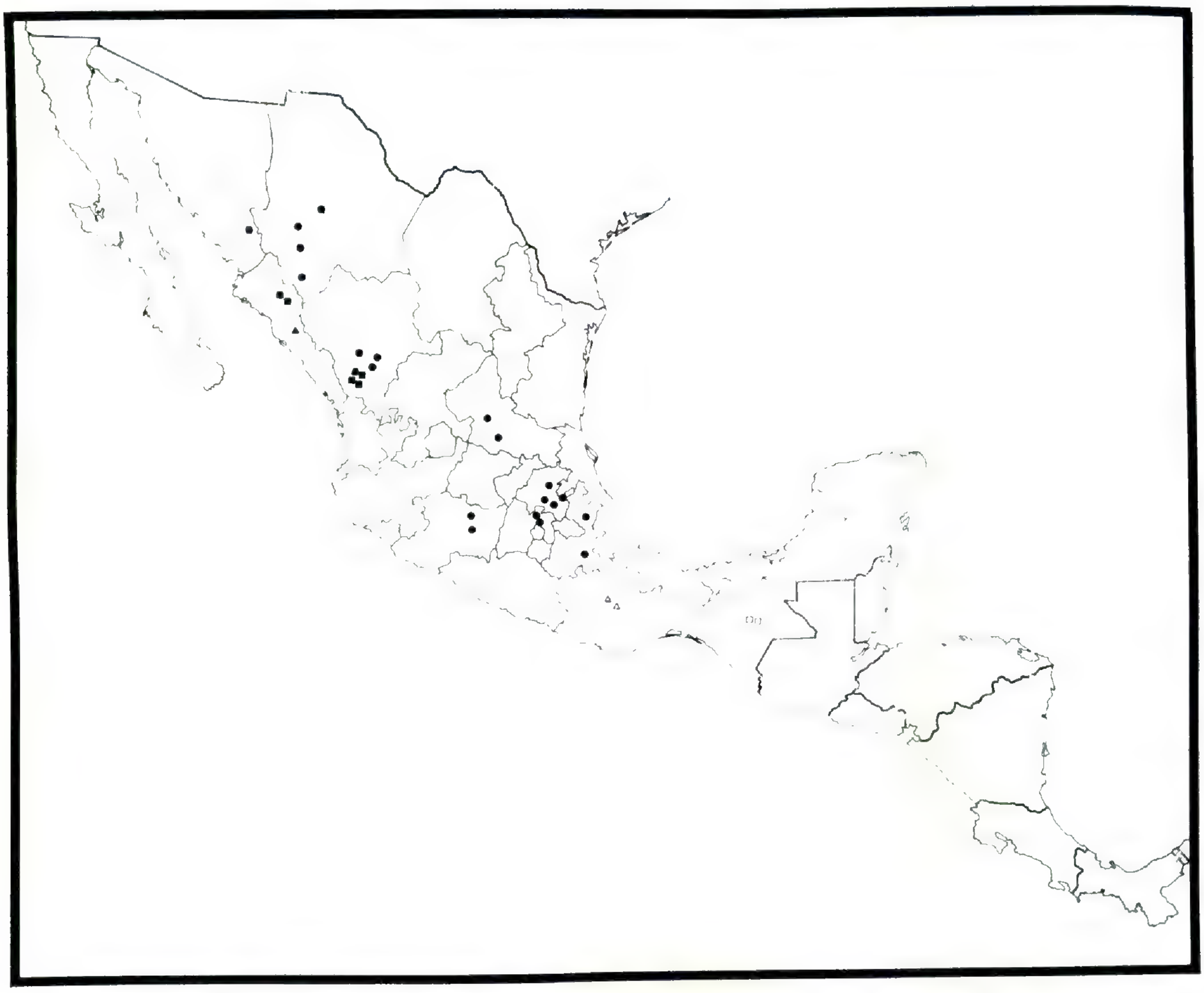
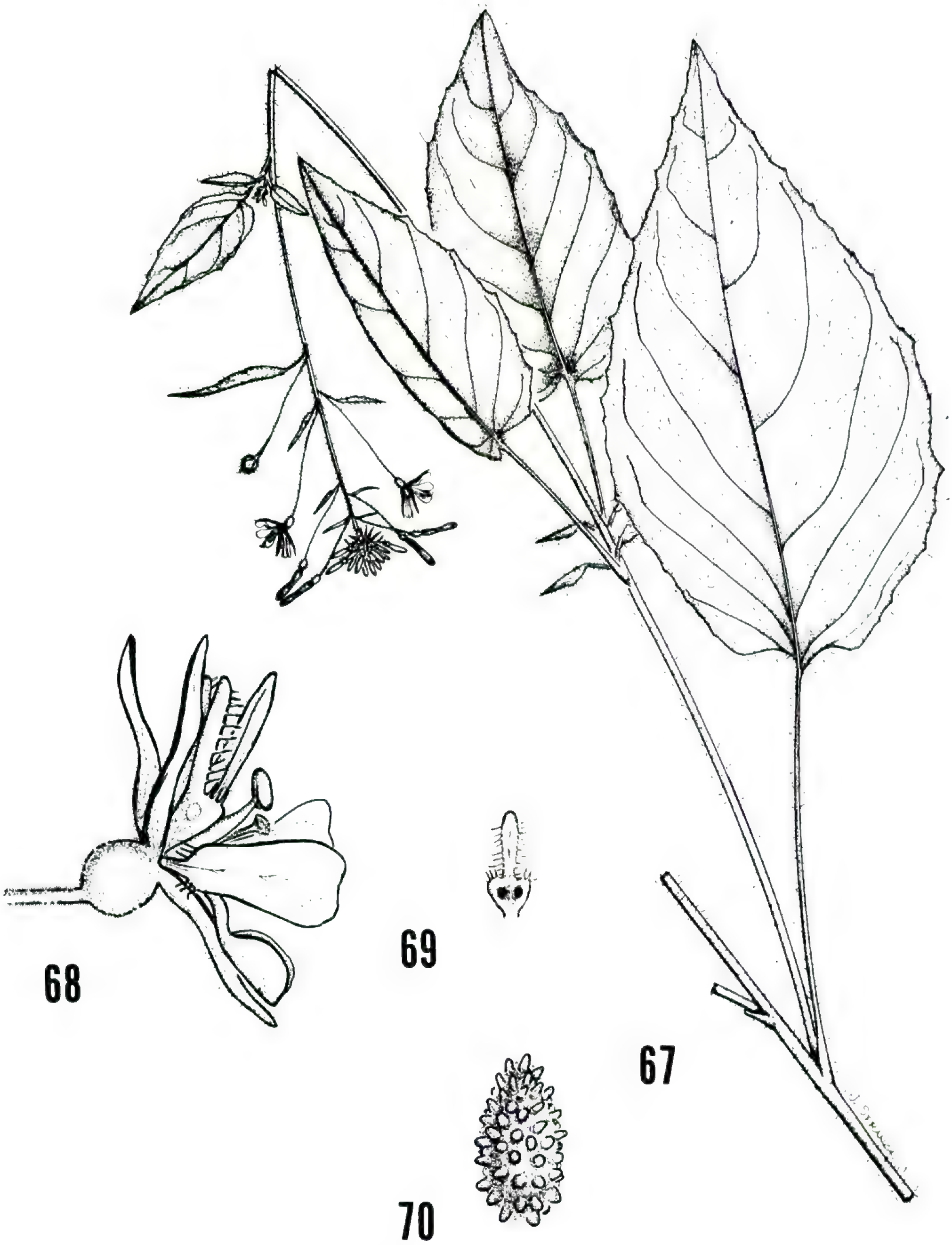


FIGURE 66. Geographical distribution of *Lopezia cornuta* (squares), *L. trichota* (dots), *L. racemosa* subsp. *moelchenensis* (open boxes), *L. conjugens* (filled triangle), and *L. smithii* (open triangles).

northern type and *L. gracilis* resemble each other to a degree, although *L. cornuta* has ± hirsute and angular stems and generally longer leaves and petioles, and therefore they have sometimes been confused. These species are amply different in the morphology of flowers and fruits as well as in their biology. *Lopezia cornuta* has longer floral parts, its pinkish-red petals, the upper ones with two glands each, its larger, angular and horned capsules, and its coarsely wrinkled-tuberculate seeds. The southern group, on the other hand, consists of plants that are somewhat similar to those of *L. racemosa*. The flower in general and the upper petals in particular are reminiscent of those of *L. racemosa*. In many details, however, *L. cornuta* is quite similar to *L. miniata* (*e.g.* leaves subentire, lower petals somewhat crenulate, upper petals biglandular). It may have been derived from populations similar to those of *L. miniata*.

12. **Lopezia ciliatula** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 279. 1973.—FIGS. 67–70.

Hirtellous annual *herbs*, ± gray-green in hue, the hairs incurved or straight. *Stems* 4–9 dm tall; branches obscurely angled. *Leaves* 1–9 cm long and 0.5–5 cm wide, ovate, or oblong-ovate to lanceolate, subcordate to obtuse or broadly cuneate



FIGURES 67–70. *Lopezia ciliatula*.—67. Branch, × 66.—68. Flower, × 6.6.—69. Upper petal, × 3.3.—70. Seed, abaxial view, × 26. All from the type collection.

at the usually oblique or unequal base, acute to acuminate at apex, serrate to serrulate, with 4–8 veins on each side of midrib, hispidulous and glandular, sometimes with a few longer appressed hairs, ciliate; petioles 0.3–6.5 cm long, very narrowly winged, pubescent. *Bracts* 3–25 mm long and 0.5–7 mm wide; pedicels

8–15 mm long, angular or narrowly marginate, spreading or ascending, densely hirtellous and glandular-pubescent. *Flowers* mainly autogamous, retaining the snapping mechanism but the anther soon shedding pollen directly on the stigma, their maturation simultaneous. No visible nectar secretion. *Sepals* 3–4.5 mm long and 0.6–1 mm wide, sparsely hirtellous and glandular-pubescent to subglabrous. *Lower petals* 2.5–4 mm long and 1.5–2 mm wide, oblong-obovate, short-clawed, subcrenulate, long-ciliate near base, white or faint pink; upper petals 2.5–4 mm long and 0.5–0.9 mm wide, narrowly linear-spatulate, slightly narrowed toward base, then broadly obtriangular-obovate, conspicuously auriculate, sessile, obtuse at apex, long-ciliate, with 2 green glands at level of auricles, white, lined with pink. *Fertile stamen* 3–4 mm long; filament winged-dilated except at the twisted apex; anther 1–1.3 mm long, faintly greenish. *Staminode* white, 2.5–4 mm long and 1.5–2 mm wide, suborbicular or obovate-spatulate, ± emarginate at apex, abruptly narrowed into a rather long claw, white or pale pink. *Style* white, 2.5–3.5 mm long; stigma 0.25–0.5 mm in diameter; ovary globose to ellipsoid, pubescent with erect glandular and eglandular hairs. *Capsule* 1.5–3.5 mm long, 1.5–3.5 mm thick, subglobose, with an admixture of glandular and eglandular hairs. *Seeds* 0.8–1 mm long, 0.4–0.5 mm thick, ovoid, distinctly papillose-tubercled, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Sinaloa, Sierra Surutato, Cañon de Tarahumares between Arroyo Verde and Rancho Tarahumares, steep north-facing slope, ca. 1100 m elevation, 27 February 1968, *D. E. Breedlove 15921* (DS).

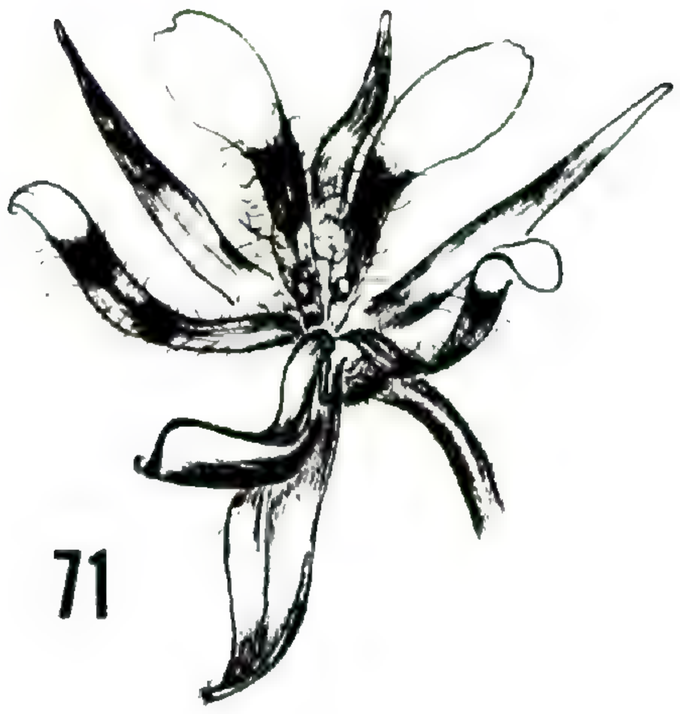
Distribution (Fig. 34): Known only from two localities, steep-walled canyons with *Bursera* and *Ipomoea*, in the Sierra Madre Occidental, Durango and Sinaloa, Mexico, 1100–1250 m elevation. Flowering, February and March.

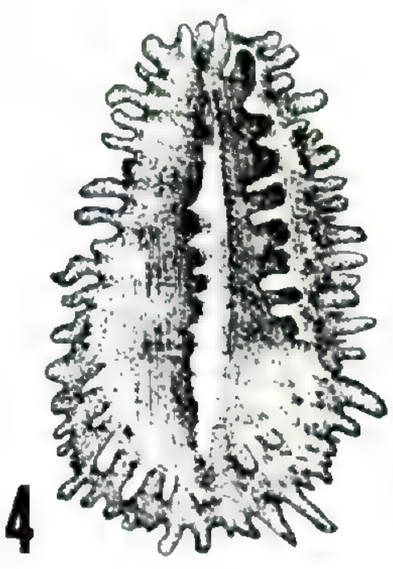
Additional specimens examined:
MEXICO. SINALOA: Cañon de Tarahumares between Arroyo Verde and Rancho Tarahumares, *Breedlove 16439, 19107* (both CAS); mouth of the Canon Tarahumares at El Alamo, *Breedlove 19058* (CAS). DURANGO: Steep side canyons of the barranca of the Río Tamazula between La Bajada and La Junta, 1250 m, *Breedlove 24491* (CAS).

Lopezia ciliatula is easily distinguishable from the related biglandular species by such features as its small flowers, sessile and basally winged-auricled upper petals, ciliation of petals, pubescence of petioles, pedicels and capsules. It has the same chromosome number as *L. cornuta*, but in overall morphological appearance it resembles *L. miniata*, from which it may have been derived. Curiously, it is known only from the same two areas as *L. suffrutescens*.

13. **Lopezia trichota** Schlecht., Linnaea 12: 273. 1838. Munz, Brittonia 13: 85. 1961; N. Amer. Fl. II. 5: 21. 1965.—FIGS. 71–74.

Subglabrous perennial *herbs*. *Roots* thick, tuberous, fleshy. *Stems* 2–10 dm tall, to 6 mm thick, angular. *Leaves* fleshy, 1–4.5(–5.5) cm long and 0.3–2.5(–3.3) cm wide, rounded or obtuse and ± asymmetrical at base, acute at apex; lower leaves ovate, serrate or serrulate, glabrous, few-veined; the upper ovate to rarely lanceolate, serrulate or subentire, subglabrous but somewhat puberulent at margins or sometimes strigulose along midrib; petioles 0.2–2.5 (–3) cm long, ca. 0.1 cm thick, slightly pubescent to glabrous. *Inflorescence* ± puberulent-strigulose;





FIGURES 71–74. *Lopezia trichota*.—71. Flower, × 3.2.—72. Capsule, × 3.2.—73. Seed, abaxial view, × 21.—74. Seed, adaxial view, × 21. All from *Rzedowski 6896* (DS).

bracts 2–15(–25) mm long and 0.5–2(–4) mm wide, ± ciliolate at margins, puberulent; pedicels 6–20 mm long, patent to almost erect, pubescent to subglabrous. *Flowers* white with deep purplish-red marking. *Sepals* 5–7.5 mm long, and 0.7–2 mm wide, ± crisp-pubescent or slightly puberulent to glabrous. *Lower petals* 4–5.5 mm long and ca. 1 mm wide, linear, obtuse and glabrous at apex, densely ciliate with curly hairs along margins; upper petals 4–7.5 mm long and 1.5–3 mm wide, obovate-spatulate, clawed for almost one-third of their length, rounded or somewhat retuse at apex, ciliate along blade except for the uppermost part, white toward apex, red below; claw ± ciliate, bearing a single gland but sometimes with an adjacent second (reduced) one. *Fertile stamen* 4–5 mm long, purplish-red; filament fleshy, glabrous; anther ca. 2 mm long. *Staminode* 4–6 mm long, and 2–3.5 mm wide, spatulate with a broad blade, clawed-narrowed at base, retuse and mucronulate at tip, purplish-red, glabrous. *Style* 4–5 mm long, crisp-pilose; stigma ca. 0.5 mm in diameter; ovary 1.5–3 mm long, 1–2 mm thick, subglobose, ± crisp-pubescent or puberulent to glabrous. *Capsule* 4–7 mm long, 3–6 mm thick, oblong-ovoid to globose, ascending, subglabrous; valves coriaceous, intact or open at apex only. *Seeds* ca. 1 mm long, ca. 0.6 mm thick, subovoid, with wing-like margins, coarsely tubercled and wrinkled, black. Gametic chromosome number, $n = 10$.

TYPE: Mexico, Hidalgo, Mineral del Monte (ca. 25 km E of Ixmiquilpán), Cuesta Blanca, rocky places, August 1836, *C. Ehrenberg 626* (HAL).

Distribution (Fig. 66): Common on dry slopes and barrancas, chiefly in pinyon-juniper woodland, in widely scattered localities from Chihuahua to Puebla, Mexico, (1200–)1600–2700 m elevation. Flowering, July to October.

Representative specimens examined:

MEXICO. CHIHUAHUA: Mts. near Chihuahua, *Pringle 733* (BM, G, GH, K, MEXU, MO, NY, P, RSA, S, UC, US, W); San Mateo to Quasarachi, *Goldman 147* (GH, NY, US); Sierra Azul, SW of Mapula, *Pennel 18656* (NY, US). DURANGO: 9 mi. SE of Santiago Papasquiaro on road to Canatlán, *Breedlove 15542* (DS); 16 mi. W of Durango on Mex. Hwy. 40, *Breedlove 14392* (DS); Durango and vicinity, *Palmer 588* (BM, G, GH, MO, POM, S, UC, US). SAN LUIS POTOSÍ: Cerro Verde, W of San Lorenzo, *Rzedowski 6856* (DS, IPN, MEXU, MICH, RSA, TEX); NE of Laguna Seca, *Rzedowski 6330* (IPN); Convalli, *Schaffner 641* (GH, NY). HIDALGO: NE of Pachuca, *Rzedowski 17059* (IPN, MEXU, MICH); Cerro Ventoso, Pachuca to Real del Monte, *Rzedowski 20575* (DS), *Pringle 9798* (GH, MO, NY, US, Z), *Rose &*

Painter 6692 (US); Cuesta de Texquedo, Tasquillo to Zimapán, *Moore 1656* (GH); Above Metzquititlán, to Zacualtipán, *Moore 5405* (UC); Sierra de Guadalupe, near Cuautepec, *Galicia*, 1962 (DS, IPN, TEX). MICHOACÁN: Near Morelia (Punguato), *Arsène 6644* (MO, US); Guanajuato to Dolores Hidalgo, *Solbrig & Ornduff 4516* (RSA, UC). MÉXICO: Near Presa de la Concepción, Tepotzotlán, *Rzedowski 22901* (IPN); Huixquilucán, la Presa "El Capulin," *Rzedowski 25863* (DS). DISTRITO FEDERAL: Santa Catarina, near Los Reyes, *Paray 1591* (IPN); Sierra del Guadalupe, *Miranda 3850* (MEXU). PUEBLA: San Luis Tultitlanapa, *Purpus 3398* (BM, GH, MO, NY, UC, US); Villa Juárez, *Galván*, 1963 (IPN).

Lopezia trichota is quite uniform morphologically and very distinctive biologically. Though maintaining the snapping mechanism and protandrous, it is very likely self-pollinated to some degree as well. The mature capsules are ± indehiscent, their coriaceous valves frequently remaining almost intact; they might, therefore, be dispersed by water. In accordance with its dry habitat, the capsule probably needs some moisture for dehiscing (partly hygrochastic); all other species of *Lopezia*, as far as known, have xerochastic fruits. *Lopezia trichota* is vegetatively propagated by its unique tubers, which are thick, fleshy and bulbous, and very different from those of other tuberous *Lopezia* species; such tubers are an evident adaptation to dry habitats. The plant goes dormant for several months, like many cryptophytes, and starts sprouting in the early summer (rainy season). Dry conditions enhance its flowering. Another distinctive feature of this species is the number of glands on the upper petals. Usually there is a single one, yet sometimes a second smaller one is developed. This suggests that its ancestors might have had two glands on each of the upper petals. Otherwise the flower, in general, resembles that of *L. racemosa*.

Lopezia trichota is restricted to central Mexico, east of the Sierra Madre Occidental and north of the Sierra Madre del Sur. Its distribution is ± interrupted (no records from Tlaxcala, Zacatecas, Aquascalientes and Queretaro), presumably because of its specific ecological demands.

14. **Lopezia racemosa** Cav., Icones 1: 12, *t. 18*. 1791. Munz, Brittonia 13: 86. 1961; N. Amer. Fl. II. 5: 22. 1965.

Annuals or *perennials*, hirsute, strigulose, or mixed strigulose and glandular-pubescent to subglabrous. *Stems* erect or ascending or decumbent and rooting at nodes, subterete, 1–15 dm tall. *Leaves* variable in size, shape and pubescence; lower leaves 1–8 cm long and 0.5–4.5 cm wide, ovate to narrowly lanceolate, acute or cuneate to rounded at base, sometimes acuminate, subacute or sometimes subacuminate at apex, mucronulate, acutely dentate or serrate to shallowly or remotely so, with 4–11 veins on each side of midrib, densely hirsute or strigose to sparsely so, with hairs usually appressed but sometimes spreading, equally pubescent on both sides to more densely so below especially along veins, sometimes subglabrous; upper leaves 0.5–5 cm long and 0.15–2.5 cm wide, ovate to very narrowly lanceolate, acute or cuneate to obtuse at base, usually acute or acuminate at apex, serrate to subentire, with (0–)3–7 veins on each side of midrib; petioles 0.1–4 cm long, infrequently narrowly winged, strigulose or more rarely subglabrous. *Bracts* 2–25(–30) mm long and 0.5–9(–12) mm wide; pedicels 6–24(–30) mm long, spreading to ascending-erect in flower, drooping to ascending in fruit, sometimes divaricate but bent upwards, strigulose or puberulent to

glabrescent. *Flowers* strongly protandrous, but in some strains self-pollinating in due course. *Sepals* 3.5–7.5 mm long and 0.5–2 mm wide, glabrous or sparsely hirsute with few long hairs especially toward apex, sometimes glandular-puberulent. *Petals* variable in size, color and inclination, whitish or pinkish-lilac to pink or red or even purplish, sometimes white-lilac or orange-red, somewhat darker near the center (lower petals) or near tip (upper petals) and paler below; lower petals (3.5–)4–9(–10) mm long and (1.5–)2–5.5(–6) mm wide, oblong-obovate or spatulate to obovate or even oblate, acuminate symmetrically or not, clawed with claw as long as or longer than blade, round and entire or nearly so at apex; upper petals 4–8.5 mm long and 0.7–2 mm wide, linear-oblanceolate to oblong-oblanceolate, erect, clawed with claw shorter than blade and ciliate to hardly so, ± obtuse and entire at apex, blade dilated to obtusely short-auricled at base, bearing a single gland; gland tiny or prominent, variable in shape, usually green, sometimes pink. *Fertile stamen* 3–5.5 mm long; anther 1–2 mm long, greenish-grey to bluish or even purplish. *Staminode* 3–5(–6)mm long and 2–3 mm wide, generally obovate, abruptly narrowed into a linear claw, ± retuse at apex, whitish to pink or red. *Style* 2.5–4.5 mm long, glabrous; stigma (0.4–)0.5–1.1(–1.7) mm across, white to pink; ovary subglobose, glabrous. *Capsule* (2–)3–7 mm long, 2–5 mm thick, usually globose, sometimes obpyriform and subclavate or ovoid or oblong-ellipsoid, rarely compressed at apex, glabrous. *Seeds* (0.8–)0.9–1.2(–1.3) mm long, (0.6–)0.7–0.8(–0.9) mm thick, ovoid, irregularly rugose- or muricate-tubercled, brown. Gametic chromosome numbers, $n = 10$ (11), 20.

Distribution (Figs. 66, 75): Widespread and common in the pine-oak zone but also common as a roadside weed and as a weed in *milpas*, from Durango (Chihuahua?) and San Luis Potosí in Mexico south to El Salvador, 1100–3300 m elevation. *Lopezia racemosa* occurs sympatrically with *L. miniata* at a number of localities. Flowering, mainly from August to March, although occasional individuals may be found in flower in any month of the year.

This extraordinarily polymorphic species includes one well marked geographic race, the tetraploid derivative subsp. *moelchenensis* of Chiapas, Mexico, and northwestern Guatemala. As reported elsewhere (Plitmann, Tai & Raven, 1974), a tetraploid plant of subsp. *racemosa* has likewise been found in Chiapas, and interploid hybridization between the two subspecies, with incomplete pollen sterility, is apparently frequent. Intermediate forms between these two are, for example: *Standley 22876* from El Salvador; *Brenckle 47280, 47396, Kellerman 4816* from Guatemala; *Matuda 5212, Shilom Ton 651, 758* from Chiapas. These specimens, although usually hirsute-pubescent, have leaves, colors, racemes and sometimes capsules or seeds as in subsp. *moelchenensis* but otherwise resemble subsp. *racemosa* (in habit, pubescence, floral morphology, and pollen). Other specimens share some features of subsp. *moelchenensis* (color of stems or flowers, serration of leaves, shape of capsule, racemes or general habit); those are considered as transitional convergent forms of subsp. *racemosa*. Collections of such subsp. *racemosa*-like plants with a few traits of subsp. *moelchenensis* are: *Shilom Ton 1482, Breedlove 7134, 7155, 11425, 12622, 8759, Breedlove & Raven 13294/3,*

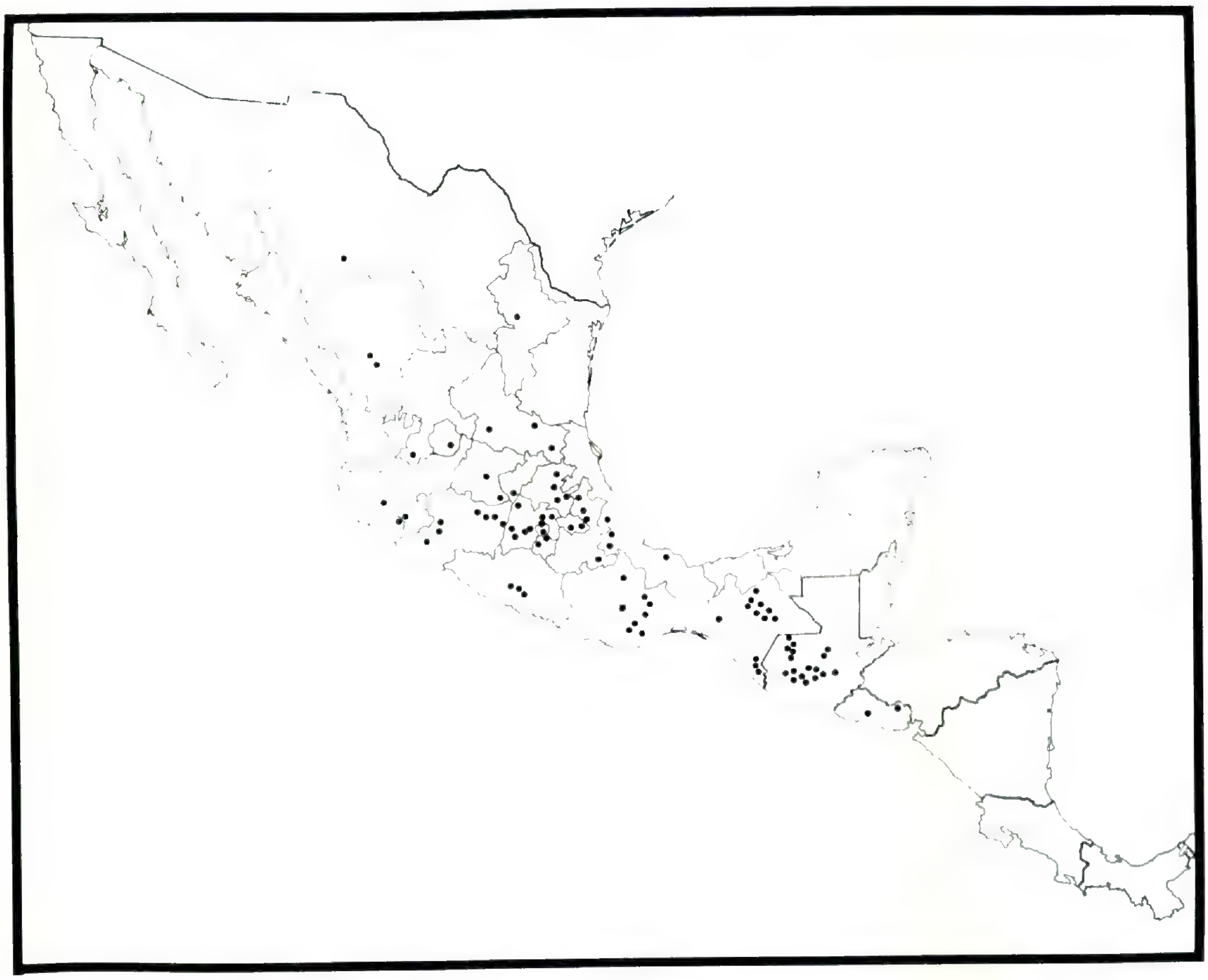


FIGURE 75. Geographical distribution of *Lopezia racemosa* subsp. *racemosa*.

Kerber 391, *Matuda 2383*, *2540*, *479*, *697*, *Miranda 4975* from Chiapas; *Skutch 1520*, *Kellerman 7613*, *Rodríguez 2041*, *Beaman 3949* from Guatemala; *Standley 22804* from El Salvador; and probably *Rzedowski 18568* from Guerrero and *Moore 2401* from Hidalgo.

Further indication of actual hybridization in the field is provided by *Shilom Ton 651*, from Paraje Pahal Ton, Municipio Tenejapa, Chiapas. This collection is of tall plants with the erect stems generally associated with *Lopezia racemosa* subsp. *racemosa* but with other features as in subsp. *moelchenensis*. Two plants were grown in the greenhouse from seeds removed from this specimen. Both of these were about 1.5 m tall, with almost simple, erect stems, relatively narrow but fleshy leaves, and orange flowers as commonly found in subsp. *moelchenensis*. One of these plants was hirsute, the other glabrescent.

Crossing experiments showed that *Lopezia racemosa* subsp. *racemosa* is comprised of lines of high and low crossability with each other. On the other hand it is amazing that many strains were quite easily crossed with the tetraploid *L. racemosa* subsp. *moelchenensis*. In such triploid hybrids, the characteristics of the tetraploid subsp. *moelchenensis*, not surprisingly, are predominant over those of the diploid subsp. *racemosa*.

KEY TO THE SUBSPECIES

Stems ascending or erect, rarely decumbent; leaves not fleshy, pubescent or rarely subglabrous, ovate or lanceolate; petals ± orange; pollen almost entirely 3-porate; widespread ..... 14a. subsp. *racemosa*

Stems decumbent, rooting at the nodes; leaves fleshy, subglabrous, mostly narrowly lanceolate; petals mostly without orange tinge; pollen with a high proportion of 4-porate and some 5-porate grains; Chiapas, Mexico, and Guatemala ..... 14b. subsp. *moelchenensis*

14a. **Lopezia racemosa** subsp. **racemosa**.—FIGS. 12–13.

Lopezia mexicana Jacq., Ic. Pl. Rar. 1: *pl. 203*. 1793.
Lectotype: Jacq., Pl. Rar. 2: *t. 203*. 1792–3. Cultivated from seeds from Mexico, probably of the same stock of the original *L. racemosa* (W—Hort. bot. Vind., Hb. Jacq., authentic?).

Pisaura automorpha Bonato, Pisaura 7, *t. 1*. 1793. Type: G.4505 (W, cultivated from the authentic?).

Lopezia hirsuta Jacq., Obs. Bot. 5: 5, *pl. 15, fig. 4*. 1796. Lectotype: Jacq., Obs. Bot. 5: *pl. 15, fig. 4*. 1796. Munz, Brittonia 13: 88. 1961; N. Amer. Fl. II. 5: 23. 1965.

Lopezia mexicana Jacq. var. *hirsuta* (Jacq.) Willd., Sp. Pl. 1: 18: 1797.

Lopezia coronata Andrews, Bot. Rep. 8, *t. 551*. 1808. Lectotype: Andrews, Bot. Rep. 8, *t. 551*. 1808. Cultivated from Mexican material of unknown origin in the conservatory of the Countess de Vandes, "Introd. 1805 by Messrs. Lee and Kennedy" (Aiton & Aiton, Hort. Kew. ed. 2, 1: 10. 1810); (E, authentic?). Munz, Brittonia 13: 88. 1961; N. Amer. Fl. II. 5: 22. 1965.

Lopezia axillaris Thunb. *ex* Schweigger, Königsberger. Arch. Naturwiss. Math. 1: 236. 1811–12. Schweigger, Enum, Hort. Regiomont 44, adnot. 26. 1812. Type: Cultivated (UPS? Non vidimus).

Lopezia mexicana Jacq. var. *coronata* (Andr.) DC., Cat. Hort. Monsp. 39. 1813.

Lopezia cordata Hornem., Hort. Hafn. 949. 1815. Type: Cultivated from seeds introduced in 1813 (C? Non vidimus).

Lopezia minuta Lag., Gen. & Sp. Nov. 1. 1816. Type: "Praedicto nomine accepimus ex Hort. Paris ann. 1815" (P? Non vidimus).

Lopezia oppositifolia Lag., Gen. & Sp. Nov. 1. 1816. Type: Cultivated from seeds sent by *D. V. Cervantes* in 1814 (= *L. annua* hortul.) (G-DC? Non vidimus).

Lopezia minima Lag. *ex* Schrank, Nova. Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 9: 92. 1818. Type: Unknown. Munz, Brittonia 13: 90. 1961.

Lopezia integrifolia DC., Prodr. 3: 62. 1828. Type: Mexico, *Alaman* (G-DC, lectotype, Munz, Brittonia 13: 87. 1961; isolectotype, US).

Lopezia lineata Zuccarini, Pl. Nov. Cogn. 2: 339. 1838. Type: Cultivated in Münich, "Crescit in Imperio Mexicano, unde semina misit clar. de Karwinski" (M, ex herb. Zucc., 1835, probably from the authentic material).

Lopezia haematodes Kunze, Linnaea 17: 579. "1843" (1844). Type: November or December, 1843, Hort. Lips. (BM, lectotype, from the cultivated authentic material which had been grown in 1842–43 in hort. bot. univ. Lips.; HAL, syntype, coll. by G. Kunze in Nov. 1843, as plant cult. in hort. bot. Lips., from Mexican seeds sent by Schleiden, 1843).

Lopezia albiflora Schlecht., Linnaea 24: 696. 1851. Type: Cultivated in hort. Hal. Sax. (HAL? Non vidimus).

Lopezia angustifolia B. L. Robins., Proc. Amer. Acad. Arts 27: 168. 1893. Type: Mexico, San Luis Potosí, Las Canoas, 30 October 1891, *C. G. Pringle 3990* (GH; isotypes, BM, F, G, IPN, K, M, MO, NY, P, POM, S, UC, US, W, Z). Munz, Brittonia 13: 90. 1961; N. Amer. Fl. II. 5: 23. 1965.

Lopezia foliosa T. S. Brandegee, Zoë 5: 250. 1908. Type: Mexico, Veracruz, Barranca de Tenampa, near Zacuapán, November 1906, *C. A. Purpus 2303* (UC; isotypes, BM, GH, MO, NY, P, US).

Lopezia elegans Rose, Contr. U. S. Natl. Herb. 12: 298, *fig. 40*. 1909. Type: Mexico, San Luis Potosí, Álvarez, 28 September–3 October 1902, *E. Palmer 159* (US 397,706; isotypes, GH, MO, NY, UC).

Lopezia glandulosa Rose, Contr. U. S. Natl. Herb. 12: 298, *fig. 41*. 1909. Type: Mexico, Zacatecas, between Bolaños and Guadalajara, 20 September 1897, *J. N. Rose 3034* (US 301,991. Isotype, NY).

Lopezia parvula Rose, Contr. U. S. Natl. Herb. 12: 300, *fig. 44*. 1909. Type: Mexico, Durango, near La Providencia, November 1898, *E. W. Nelson 4987* (US 333,016. Isotype, GH).

Lopezia pringlei Rose, Contr. U. S. Natl. Herb. 12: 300, *fig. 45*. 1909. Type: Mexico, Oaxaca, Sierra de San Felipe, 25 September 1894, *C. G. Pringle 6005* (US 461,987. Isotypes, BM, F, G, IPN, M, MEXU, MICH, MO, NY, P, RSA, S, UC, W, Z).

Lopezia corymbosa Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Guatemala, Alta Vera Paz, Cobán, November 1885, *von Türckheim 766* (K. Isotypes, GH, NY, P, US).

Hirsute, strigulose, or mixed strigulose and glandular-pubescent to subglabrous annual or perennial *herbs*. *Stems* ascending or erect, rarely decumbent, pubescent or subglabrous. *Leaves* not fleshy, pubescent or more rarely subglabrous, 0.5–8 cm long and 0.15–4.5 cm wide, ovate or lanceolate, acute or cuneate to obtuse at the base, acutely dentate or serrate to shallowly and remotely so, the teeth usually lacking dark clusters of "oil cells" (Stein, 1915) at the tips. *Pedicels* 0.6–2.4(–2.7) cm long. *Petals* whitish or pinkish-lilac to pink or red or even purplish, sometimes lilac-white or orange-red. *Pollen* almost entirely 3-porate. Gametic chromosome number, $n = 10$ (11, 20).

Lectotype: Cav., Icones *t. 18*. 1791, based upon plants grown in the Royal Botanic Garden at Madrid. Probable authentic material: "*L. racemosa* Cav., cult. in hort. Carolin., 1796," *Gmelin* (W) and "*Gmelin* in 1790" (W); "*L. racemosa*, ex hispania misit *D. Cavanilles* 1790–91, Herb. d'Antoine Laurent de Jussieu" (P); "*L. racemosa* Hort. Chelseam., 1796" (BM; *L. racemosa* was grown at the Apothecaries Garden, Chelsea from 1792 onward from seeds received from Madrid; Bot. Mag. 7: 254. 1797); "*L. racemosa*, Hort. R. Matr." (M; according to Munz, 1961: 87: "2 sheets, one dated 1802 and 1814, the other 'Herb. Cav.'; they are labelled *L. mexicana* Jacq., *L. racemosa* Cav., *Pisaura automorpha* Bonata, *Entomanthus* [*sic*] Sesse & Moc.; it would seem that Cavanilles' name *racemosa* and Jacquin's name *mexicana* are based on the same material, or same lot of seed from Mexico").

Distribution (Fig. 75): That of the species. Flowers mostly between April and November (the rainy season), although occasional individuals may be found in flower during any month of the year.

Representative specimens examined (additional to those listed by Munz, 1961):

MEXICO. QUERÉTARO: 1 mi. NE of Amealco, *Breedlove 7213* (DS). GUANAJUATO: Santa Rosa Mts., *Dugés 308b* (GH); Sierra NE of Guanajuato, *Ripley & Barneby 13365* (DS, NY); 10 mi. E of Jeracuaro, *Breedlove 7214* (DS). AGUASCALIENTES: 21 mi. W of Aguascalientes, *McVaugh & Koelz 153* (MICH). SAN LUIS POTOSÍ: Near San Luis Potosí, *Parry & Palmer 256 1/5* (BM, MO, NY, US); Potrerillos, Municipio of Xilitla, *Rzedowski 10001* (DS, IPN, P); 2 km N of Puerto del Hambre, Municipio of Cd. del Maíz, *Rzedowski 8310* (IPN); Sierra de Álvarez, near Puerto Huerta, *Rzedowski 5269* (IPN). HIDALGO: Between Pachuca and Real del Monte, *M. E. Moore 1565* (BM, GH, MICH, UC); 9 km W of Huauchinango, *Rzedowski 23425* (DS); 10 mi. E of Huichipán, *Breedlove 7208* (DS); 4 mi. SW of Atotonilca, *Breedlove 7203* (DS); 30 mi. S of Jacala, *Breedlove 7205* (DS); Chapulhuacán, *Sharp 441747* (RSA); Zimapan, *Coulter 179* (GH, K). JALISCO: SE slopes of Nevado de Colima, Atenguique to Tonila, *McVaugh 11725* (MEX, MICH, RSA, US); Sierra de Manatlán, SE of Autlán near Aserradero El Cuartón, *McVaugh 13830* (MEX, MICH, RSA). COLIMA: Near Volcán Colima, *H. Ross 495* (M). MICHOACÁN: 47 mi. E of Morelia, *Breedlove 7224* (DS); 20 mi. E of Morelia, *Breedlove 7225* (DS); 17 mi. S of Zinapecuaro, *Breedlove 7222* (DS); Tancitaro,

Leavenworth & Hoogstraal 1114 (MO); 2 km SE of San Miguel del Monte, *Rzedowski 25173, 25184* (both DS). GUERRERO: Cerro Alquitrán, near Mazatlán, *Rzedowski 23628, 23649, 23652* (all DS); Tlacotepec, Cerro Teotepec, *Rzedowski 18568* (IPN, MEXU, MICH); 3 km S of Amojileca, *Rzedowski 23560* (IPN). MÉXICO: 18 mi. SW of Toluca, *Molseed 546* (DS); 20 km NE of Texcoco, *Rzedowski 21423* (DS); 5 km N of Mesón Viejo, Municipio of Temascaltepec, *Rzedowski 21694, 21708* (DS); 15 mi. E of Zitacuaro, *Breedlove 8075* (DS); city limits of Lerma, *Breedlove 7201* (DS); S city limits of Amecameca, *Breedlove 15445* (DS); 28 mi. SE of San Juan del Río, *Breedlove 15451* (DS); Coyotepec, La Marquesa to Chalma, *Rzedowski 17244* (IPN); near the Pyramid of Calixtlahuaca, *Barkley, Westlund & Paxon 675* (TEX); Valle de Bravo, *Matuda et al. 26937* (MEXU). DISTRITO FEDERAL: San Angel, *E. G. Smyth 205* (US); La Venta, *Lyonnet 1432* (US); Cerro de Santa Catarina, *Paray 70* (IPN). MORELOS: Lagunas de Zempoala, *Breedlove 15835* (DS), *Holguin s.n.* (IPN), *Langman 2672A* (US), *Rzedowski 21623* (DS); Cuernavaca, *T. Beelin 50* (IPN); Cuautla, *B. Downing 160* (MICH). TLAXCALA: E of Ciudad Tlaxcala, *Ripley & Barneby 13636* (DS); between San Cristóbal and Calpulalpán, *Sohns 571* (MICH, US). PUEBLA: 7 mi. N of Atotonilco, *Ripley & Barneby 13626* (DS); Alrededores de Xicotepec de Juárez, *L. Gonzales Quintero 767* (DS); Puenta del Emperador, *Sharp 44404* (RSA); San Luis Tultitlanapa, *Purpus 4193* (UC); Huauchinango, *Rudd 2012* (DS); Chaltetela, 3 km NE of Zacapoaxtla, *Giovannini* (DS). VERACRUZ: Orizaba, *Botteri 932* (BM, K, P, RSA), *F. Muller 207* (W); Veracruz to Orizaba, *F. Muller 1573* (K); near Las Vigas, *Dodds 97* (MICH); Maltrata, *Matuda S-134* (MICH); Jalapa, *Ch. L. Smith 1786* (NY), *Schiede & Deppe 536* (MO, NY); near El Puerto, above Acultzingo, *Sharp 44832* (RSA); 5 km SE of Teocelo, *Garcia Saucedo 117* (DS); La Sabana, S of Volcán de San Martín Tuxtla, *M. Sousa S.3035* (MEXU). OAXACA: Monte Albán, *Conzatti 4858* (MICH); Cordillera, Mixteca Alto, *Galeotti 3060* (G, P); 15 km S of Sola de Vega, *Rzedowski 21324, 21343* (DS); San José del Pacífico, municipio of Miahuatlán, *Rzedowski 21003* (DS); on road from Teotitlán del Camino to Huautla, *Breedlove 15769* (DS); 15 mi. SE of Tamazulapán, *Breedlove 7186* (DS); 16 mi. N of San Gabriel, *Breedlove 9882* (DS); 1 mi. E of Ixtlán de Juárez, *Breedlove 7179* (DS); 1 mi. NW of Tamazulapan, *Breedlove 7191* (DS); 5 mi. NE of Sola de Vega, *Breedlove 8024* (DS); W slope of Mt. Zempoaltepec, *Nelson 595* (US); from Chiquihuitlán to Santa Ana Portezuelo, *Conzatti 3854* (MEXU, US). CHIAPAS: Paraje of Matsab, Municipio of Tenejapa, *Breedlove 12684* (DS); Municipio of Zinacantán, *Laughlin 2936* (DS); Colonia 'Ach'lum, Municipio of Tenejapa, *Ton 1362* (DS); near Piedracitas, Municipio of Chamula, *Breedlove 7128* (DS); NW side of Cerro Santa Cruz, Municipio of Chenalho, *Ton 1864* (DS); 7 km NW of Pueblo Nuevo Solistahuacán, Municipio of Jitotol, *Raven & Breedlove 19806* (DS); summit of Cerro San Cristóbal, Municipio of San Cristóbal de las Casas, *Breedlove & Raven 13294/3* (DS); Amatenango del Valle, Municipio of Amatenango del Valle, *Ton 1482* (DS); Fenix, *Purpus 10202* (NY, UC, US); Mt. Tacaná, *Matuda 2383* (MEXU, MICH); Mt. Ovando, *Matuda 2540* (MEXU, MICH); Fraylesca, near Siltepec, *Matuda 5212* (MEXU, TEX).

GUATEMALA. HUEHUETENANGO: Jacaltenango, *E. W. Nelson 3590* (US); Sierra de los Cuchumatanes, near San Juan Ixcoy, *Beaman 3949* (DS, GH, TEX, UC); 8 km W of Aguacatán, *Williams, Molina & Williams 21861* (G); Sierra de los Cuchumatanes, 3 km N of Chiantla, *Williams & Williams 21727* (G); road to Barillas, Municipio of Barillas, *Breedlove 8759* (DS). TOTONICAPÁN: 5–10 km N of San Carlos, *Williams, Molina & Williams 22570* (G); San Cristóbal, *Tejada 257* (US). QUEZALTENANGO: Near Santa Maria, *Naxon & Hay 3570* (US); Cuesta del Caracol, N of San Juan Ostuncalco, *Williams, Molina & Williams 22744* (G); San Martín, *Shannon 262* (K, US). SANTA ROSA: Volcán Jumaytepeque, *Heyde & Lux 4337* (G, GH, K, M, NY, US). ALTA VERAPAZ: Cobán, *J. D. Smith 1681* (G, M, MO), *H. Johnson 41* (NY), *Türckheim 367* (BM, P). QUICHE: Nebaj, *Skutch 1894* (A). SACATEPÉQUEZ: Volcán de Agua above Santa Maria de Jesus, *Standley 59386* (NY), *Bell & Duke 16965* (MICH); Pachali near San Lucas Sacatepéquez, *Anderson 4614, 4614A* (MO); 4 mi. NW of Ciudad Vieja, *Breedlove 11425* (DS). SUCHITEPÉQUEZ: Volcán Atitlán, *Skutch 1520* (GH). SOLOLA: Near Lake Atitlán, *Williams, Molina & Williams 25341* (a peculiar form; DS). CHIMALTENANGO: Near Parramos, *Standley 59882* (POM); Soledad, Volcán Acatenango, *Hunnewell 17188* (GH); Chichavac, *Skutch 11* (US). GUATEMALA: Near San Juan Sacatepéquez, *Standley 59271* (POM); Camino del Sapote, *Bernoulli 234* (G, K, NY); Volcán Pacaiya, *Brenckle 47280* (NY, S) *47396* (RSA); San Vincente Pacaya, *Tonduz 457* (G, MO, US). JALAPA: Between Jalapa and Paraíso, *Standley 77344* (POM).

EL SALVADOR. SAN SALVADOR: Volcán San Salvador, *Williams & Molina 15103* (a peculiar form; GH), *Standley 22876* (GH, NY, US), *22804* (GH, US), *Calderón 611* (US). MORAZÁN: Cordillera Miramondo, *Molina, Burger & Wallenta 16858* (W).

CULTIVATED: "*Lopezia mexicana*, hort. bot. Erlangensis 1795 & 1805" (M); "*Lopezia racemosa* hab. prope Mexico," hort. bot. Monac. 1815 (M, herb, Zuccarini; actually "*L. coronata*"); Jardin Pl. de Paris, 1818, *M. Perrottet* (G, probably from the authentic stock); "*Lopezia cylindrica* hort. bot. Paris, *Bonpland*" (G); Cult. in Serre, à la Pierrière, February 19, 1901, *Beauverd* (G); *L. coronata*, cult. in Berlin, July 1838, herb. Maire (P).

Lopezia racemosa subsp. *racemosa* is variable in almost every character, particularly in the following:

1. *Pubescence*: From densely hirsute or densely strigulose (long to short hairs, respectively) to subglabrous. Perennials are more variable than the annuals in this respect. The hairs can be erect or appressed, varying in color (whitish or rusty to purplish); some are glandular in some plants ("*L. glandulosa*"). The extent of hairiness often changes in an individual from season to season, and it frequently segregates in the progeny. Thus one can observe plants with glabrous or strigulose main stems and hirsute branches, and vice versa, or parental pubescent or subglabrous plants of which the progeny is only partly so. Very generally we can state that the most densely pubescent type is common in the south, whereas glabrescent or short-pubescent ones are more common in the north.

2. *Leaves*: As in most taxa of *Lopezia* the leaves are variable in size, shape, pubescence and serration—in individual plants as well as within and between populations—as implied in the general description. Material with relatively narrow leaves has often been determined as *L. angustifolia* or *L. lineata*. The leaves can be remotely spaced or dense ("*L. foliosa*"), persistent or early deciduous, correlated with the habit which, in turn is dependent, at least in part, on the ecological situation. The leaves are generally alternate though the lower ones and those on late branches are ± opposite ("*L. oppositifolia*"); in the related *L. conjugens* they are mostly opposite. The dentation is less pronounced in the upper leaves, and it sometimes differs from plant to plant or from population to population. The teeth can be few and remote or dense and numerous, small to large, acute to shallow ("*L. integrifolia*"). Individual and population variation is also indicated in the number of lateral veins per leaf. The petioles are variable in length (0.15–4 cm); those of the upper leaves and bracts are shorter. Long-petioled leaves are more common among the annual and/or subglabrous plants, which tend to have subangular stems.

3. *Inflorescence*: The racemes are many or few per plant, short (ca. 5 cm) to rather long (30 cm or even longer), simple or branched and then forming an open panicle or infrequently a corymbose inflorescence ("*L. corymbosa*"), leafy below ("*L. axillaris*") to hardly so. The bracts are as variable as the leaves. The pedicels vary in length (0.6–2.7 cm), in color, pubescence and inclination; they are ascending to erect or sometimes curved in flower, drooping to ascending in fruit.

4. *Flowers*: Usually there are many, usually crowded at tip, more remote below. Certain populations have few-flowered or loose racemes. The flowering rate on a single plant as well as the whole pattern of phenology show wide variation; from very gradual and/or long flowering to an almost simultaneous and/or rapid flowering, once to two or three times during the year, and from midsummer

(July) to winter or early spring. Occasional plants or populations may even flower in June.

5. *Sepals*: Variable in size, pubescence and color, and—to a lesser extent—in shape and position (usually the upper three are straight, ascending, and close to each other but sometimes they are more divaricate). The length ranges from 3.5–7 mm.

6. *Petals*: Almost as variable as the leaves. The petals vary in color, size, shape and relative position. Their color ranges from pinkish-lilac or pink to red or purplish; in Chiapas orange-flowered plants are rather common (as in subsp. *moelchenensis*). White-flowered individuals have been observed also ("*L. albiflora*" and *Breedlove 8030*). Though the variation in color is ± continuous there are two predominant forms: a) petals pinkish-lilac; these plants are often less hirsute and accordingly commoner in the north (referred to *L. racemosa* s. str. and *L. coronata*). b) Petals red (salmon or coral or purplish); often more hairy and commoner in the south (referred to *L. hirsuta* and *L. angustifolia* sensu Munz, 1961). Plants of these two sorts occur together in many of the recorded localities, and they often segregate from the progeny of a single individual. There is no evident biological barrier between them. In Guatemala, however, only red-flowered plants have been found. The variation in color parallels that of *L. miniata*; so does the variation in size of the petals, particularly the lower; their shape is also variable, even more so than in *L. miniata*. The upper petals are usually erect, but the lower may be almost divaricate or ascending to almost erect; sometimes they are ascending-divaricate with blades bent upward (then the blades are asymmetrically acuminate). The claws vary in length to a lesser extent; those of the upper petals are glabrous to distinctly ciliate-hairy. The blades are either of a single color or differ in shade in certain parts; bicolored petals are especially frequent among the pinkish-lilac type.

7. *Glands and auricles*: The upper petals lack true auricles; they are, however, slightly to conspicuously dilated at the base of the blade, above or around the gland, and sometimes even have short and obsolete, rounded auricles (but never well-developed ones like those of *L. miniata*). The glands vary in size (minute to rather large) and shape; they are usually round, but oblate or kidney-shaped ones on the one hand and ovoid or oblong ones on the other have been observed in several different populations.

8. *Fertile stamen and style*: Both vary considerably in length. The anther is variable to some extent in size and color. The pollen is mostly 3-pored, infrequently with a few 4-pored grains, which are frequent in subsp. *moelchenensis*.

9. *Staminode*: Much like the petals, the staminode varies in size and color. It might be also of the same color as the petals or of a different (paler or stronger) shade.

10. *Capsules*: Amply variable in size, less so in shape and inclination. Their dimensions range from very small, as in *L. miniata*, to very large, almost as large as in *L. trichota*. The latter are common in the sort of plants that have been called *L. coronata*. In many cases the capsules differ in size during the flowering season with the first ones usually the largest; this is partly true also for the flowers. In cultivation (or in the wild, under favorable conditions of moisture)

the capsules become on the average larger than normal. The shape is generally globose, yet plants with ovoid or oblong-ellipsoid, sometimes asymmetrical, capsules are not uncommon. There are many peculiar forms as well: obpyriform and subclavate (resembling those of *L. conjugens*), compressed at apex and apple-shaped, and ovoid-oblong or elliptic-obovoid (especially in subsp. *moelchenensis*). Certain extreme forms are explicitly recorded later. As to their inclination, the capsules either remain erect or ascending or bend into a nodding position.

11. *Seeds*: Variable in number per capsule (ca. 2–4 seeds per locule) as well as in dimensions; almost as a rule, the bigger the capsule, the more seeds (and larger ones) it contains. Some variability is pronounced in the texture of the seeds (*i.e.* size, shape and arrangement of the tubercles).

12. *Habit*: *Lopezia racemosa* includes annual and perennial strains, differing neither morphologically nor biologically and displaying almost the same wide variation. Either can be erect or ascending, procumbent or straggling. The stems vary from thick and woody to slender and herbaceous, in color (green or brownish to purple-red, in different or the same plants), in number and amount of branching; they are usually terete but sometimes (particularly in the annuals) ± angular, rigid and straight to flexible. The branches are equally variable.

Plants and populations vary in their stature; small or delicate (*e.g.* "*L. annua*," "*L. elegans*," "*L. parvula*") *vs.* huge and lush ones; stem length ranges from 10 cm or rarely less to 120 cm or even more. In several cases this variation, though genetically controlled, is obviously correlated with the habitat-conditions and changes accordingly.

Collections with many rooting stems are, among others: *Balls 5446*, *Moore 2401*, *H. Johnson 41*, *Raven & Breedlove 19806* and those of *Leavenworth*, and this habit is characteristic of subsp. *moelchenensis*.

Collections with peculiar pubescence are, among others: *Feddema 2802* from Guerrero (hirsute with partly purplish hairs, also glandular-pubescent); *Dodds 97* from Veracruz (with long-hirsute pedicels!); *Arsène* in 18.11.1909, from Michoacán (with long stiff hairs, some apparently glandular); *Flores C. 150* from Morelos (with densely and distinctly glandular-pubescent pedicels); *Rudd 2012* from Puebla (hirsute and glandulose-pubescent).

Collections with deeply and acutely serrate leaves are, among others, from Puebla (*Rose & Hay 5654*), Nuevo León, Hidalgo, México, Morelos (*Langman 2672A*), Michoacán (*Hinton 13281*), and Chiapas.

Many collections have short-petioled leaves (especially in perennials) or short-pedicelled flowers. Large, long-petioled leaves (which are probably the first ones) are common in the less hairy, angularly stemmed plants, which are frequently annual. Collections with corymbose racemes are mainly from Guatemala (*Heyde & Lux 2948*; *Naxon & Hay 3570*; *Bell & Duke 16965*); plants with leafy racemes, however, have been collected in several places throughout Guatemala and also in Chiapas. Specimens with exceptionally long pedicels are uncommon (*Abarca 67* from Teneria, México; *Bourgeau 1603* from the valley of Córdoba, Veracruz).

Collections with long racemes and/or large flowers (wide and long petals) are, among others: *Paray 1283*, *Pringle 13988*, *Rose & Painter 7240*, all from Morelos; *Abarca 67*, *Hinton 7236*, from México; *Bourgeau 1603* from Veracruz; *Conzatti 4858* from Oaxaca; *Shilom Ton 505*, *Breedlove 7155*, from Chiapas; also from Michoacán and Guatemala.

One collection, *Breedlove 8030* from Oaxaca, consists of plants with completely white flowers. Many collections, particularly from Veracruz and México, are characterized by relatively small flowers and/or capsules. Some of these morphs represent distinct populations, each with its extreme traits, most of them located either in the northern part of the range (Durango, San Luis Potosí, Aguascalientes) or the eastern parts (Veracruz, Puebla, Hidalgo, and even Morelos). In addition to the ones we have singled out for discussion, there are many other forms, unique or distinguished in other traits, such as petal width, length and ciliation of claws, pedicel inclination, seed surface, and stem morphology. Certain populations might actually be regarded as microspecies, and a few (*Soderstrom 875*, *Paray 3203*) are probably new taxa. In a few cases more material is needed for a definite evaluation; in a few others their status is yet to be experimentally determined. Altogether, it seems that most belong or are related closely to *L. racemosa* sens. lat., as a superspecies (or macrospecies).

In our greenhouse experiments we observed the occurrence of certain physiological and other strains: Strains differing considerably in the degree of self-pollination; early flowering vs. late flowering plants; different germination and growth-rates; cold-resistant strains; strains consisting of plants with two flower colors (lilac and red-pink, *Breedlove 8024*); and plants with peculiar tomato-shaped capsules (*Breedlove 9882*). These and other cryptic strains taken together add to the remarkable polymorphism of the species.

Lopezia racemosa subsp. *racemosa* is very flexible in its reproductive biology. For example, all populations have the "snapping mechanism" for pollination in spite of the fact that some of them are ultimately highly self-pollinated; moreover, the plants occasionally propagate vegetatively by adventitious roots, as in subsp. *moelchenensis*. Teratological forms have been observed as well, both in the greenhouse or in wild material, especially from Veracruz. As a rule, these forms are fasciated and sometimes their reproductive parts (racemes, sepals, etc.) have become vegetative ones (*e.g. Botteri 519 pro parte*). A doubling of petals has also been noticed in some hybrids.

In addition to the wide genetic variability in *L. racemosa* subsp. *racemosa* is its rather extreme phenotypic plasticity, particularly in response to density (habit and flowering), moisture conditions (stature, pubescence, flowering) and temperature. Such plasticity, pronounced in almost every part or stage, is typical for weedy plants (usually annuals). The variation of *L. racemosa* is therefore in accordance with its ecological requirements. This species is rather an ubiquist, occupying primary and secondary habitats, on various soils, and in different climatic conditions as reflected by its large distribution. Its variability, polymorphism, and polytypy are consistent with those of eurochoric species. *Lopezia racemosa* subsp. *racemosa* is often a colonizer, invading cultivated or disturbed lands from its neighboring natural habitats. As in many other groups of plants,

it may have been through this process that annuality became prevalent in the population.

In view of the high degree of variability in *Lopezia racemosa*, its taxonomic complexity is not unexpected. Earlier in this century, Rose (1909) and Sprague and Riley (1924) divided not only it but also *L. miniata* into a number of species. By 1961, Munz had reduced these to only four: *L. racemosa* s. str., *L. hirsuta*, *L. angustifolia*, and *L. coronata*. The delimitation of these taxa, however, is based upon various inconstant, variable and uncorrelated characters (*e.g.* dimensions of flowers and capsules). Several plants or populations do indeed fit into the typical diagnoses, which is why taxonomists, with the scanty material they had and little biological information, treated them separately; many other populations are intermediate between these morphological modes. Munz (1961: 87–88) was already aware of this problem, listing certain "plants suggesting hybridity with *L. mexicana* and *L. angustifolia*," and pointing out that some forms of *L. racemosa* approach *L. hirsuta* "with which it may well hybridize." Though we consider all four units as one species, it is relevant to discuss them briefly one by one.

Lopezia racemosa s. str. is still the most variable taxon, which includes most of the synonymous specific units. This "species" is common in the state of México and characterized as follows: Annuals, pubescent to glabrescent; stems rather coarse, angular, usually branched; leaves ovate or broadly lanceolate; racemes simple or paniculate; pedicels ± glandular-pubescent, ascending to reflexed (pending), axillary in bracts; upper petals linear or linear-oblong, obtuse; lower petals long-clawed, spatulate; capsule globose, 3.5–4.5 mm in diameter.

The original descriptions of *L. racemosa* and *L. mexicana* are quite general, covering the whole group. Any other differentiating characters (*e.g.* habit or stature, number of veins on leaves, length of racemes, branching dimensions of floral parts) are rather imposed than natural. Some representative collections of typical "*racemosa*" are, for example: *Pringle 6580*, *Purpus 1697*, *Munz 15055*, *Breedlove 7201*, *Rzedowski 23325*, *Rose & Painter 7277*, *Weaver 976*, *Sohns 571*, *Bourgeau 767*. Most of the rest of the material combines certain traits of the other categories.

Plants of the sort that have been called *Lopezia hirsuta* are very common throughout Mexico, particularly in the southern states of Chiapas and Veracruz. They are characterized as follows: Mostly perennials; stems terete, suffruticose, hirsute; leaves ovate to lanceolate, hirsute-pubescent especially beneath, remotely or shallowly serrulate; racemes leafy at base; flowers of one color; capsule ca. 3 mm in diameter.

As discussed, pubescence, color of petals, size of capsule are not sufficient for species delimitation and actually many hirsute plants share some features with "*racemosa*" or "*angustifolia*." Some collections of typical "*hirsuta*" are, for example: *Pringle 2973*, *8127*, *Rzedowski 7143*, *Galeotti 3034*, *Balls 5446*, *Hinton 15464*, *11280*, *Purpus 1696*, *6803*, *Rose & Painter 7240*, *Breedlove 7030*, *Nelson 1338*, *Conzatti 3854*, *Bernoulli 234*, *Standley 59882*, *59386*. There are many hirsute annuals as there are "*racemosa*" perennials; red petals of one color, however, are more frequent in perennial or hirsute plants.

Lopezia coronata is characterized as follows: Annuals, subglabrous to pubescent; stems long, simple; leaves broadly to narrowly lanceolate, glossy, serrate; petioles somewhat decurrent; racemes simple, leafy, crowded at tip; pedicels spreading to recurved in fruit; flowers axillary, a little large in all parts; petals redder at base, whiter at apex; staminode whitish; capsule up to 8 mm long and 6 mm wide, globose or ovoid to obovoid.

The original drawing and description are based upon "a plant in the conservatory of the Countess de Vandes"; *i.e.* on a cultivated plant. In addition, Andrews made the point that "*Lopezia coronata* is . . . of recent introduction." Munz noted as well that he had found relatively few herbarium specimens collected in the wild and that "the status of this plant has been and still remains somewhat doubtful. In cultivation for about a century and one-half, it seems quite distinct from *L. racemosa*. . . ." We do agree that it is a form different from many others, yet in our opinion it is simply a cultivar of *L. racemosa*. The wild material cited by Munz (*Wawra 950*, *Standley 22804*, *22876*, *Purpus 6805*) is either *L. racemosa* subsp. *racemosa* or *L. racemosa* subsp. *moelchenensis*. This cultivar was introduced in many European botanical gardens as early as 1805 (Aiton, 1810, vol. 1, p. 10). *Lopezia racemosa* had been introduced into botanical gardens in 1791 and was widespread in cultivation by 1796. Andrews, unaware of the variability and polymorphism in that group, regarded *L. coronata* as a distinct species.

Apart from *Lopezia coronata* there are a few other cultivars, one of which is *L. lineata* Zucc., which in habit is intermediate between *L. racemosa* and *L. angustifolia*: hirsute-pubescent, with small upper leaves, glabrous pedicels but somewhat pilose sepals, petals violet-white. Plants of this sort have been in cultivation since about 1837. Zuccarini based his diagnosis and observations on plants grown from seeds taken from Karwinski's Mexican collection. He drew the distinctions between this taxon and the related ones (*L. racemosa*, including *L. coronata* and *L. hirsuta* or "*L. tuberosa*"), distinctions which we now consider insignificant.

Another cultivar is *Lopezia cordata* Hornem., which according to the author was introduced into cultivation 1813 and is distinguished from *L. racemosa* by having some subrotund-ovate-cordate leaves and purple flowers, plus a few minor traits. Undoubtedly this taxon is synonymous with *L. racemosa*.

Lopezia minima Lag. *ex* Schrank is also known from cultivation, together with *L. coronata*, and they are apparently identical. Many plants of *L. racemosa* s. str. display certain characteristics of *L. coronata*; typical collections of the latter, all of cultivated specimens, are for example: *Lopezia coronata*, herb. Fenzl (W), herb. M. E. Moricand (G), herb. Gadeceau (BM), ex horto bot. Petropolitano (US), from hort. Copenhagen (S), herb. H. Van Heurck (P), herb. Tho. Clark (K), *Lopezia coronata* Andr. and *L. axillaris* Thunb., from H. Ups. (S), and from Bern in 1927, Meisner herb. (NY).

Lopezia angustifolia is characterized as follows: Shortly pubescent to glabrescent perennials; stems ± angular and purplish, branched; leaves narrowly lanceolate or oblanceolate to linear, shorter than usual, the upper ones a little

smaller, narrow; petioles short; petals purplish, the upper with a broad gland; capsules oblong-ovoid; inflorescence branched, racemes many.

The type collection (*Pringle 3990*) is closer to *L. racemosa* s. str. than to *L. hirsuta*, and in some respects (stems, capsules) it resembles *L. nuevo-leonis*. There are only a few similar collections, mostly from San Luis Potosí (*Palmer 159*, type of *L. elegans*), and probably these are populations typical of and limited to that part of Mexico. Subsequent to the original description, Munz (1961) unjustifiably broadened the description, emended it, and included plants of the sort that have been called *L. foliosa* in *L. angustifolia*. Except for the branched habit, the narrower leaves, and probably the somewhat smaller flowers there is no evident similarity between these two taxa. *Lopezia foliosa* is more related to "*L. hirsuta*," by such features as its hirsute to pubescent habit, subterete and rooting stems, and small capsules. It is distinguished by its smaller leaves, shallowly serrate to entire, shorter floral parts and densely leafy branches. Populations of this kind, though less leafy and more hirsute, are common in the state of Veracruz, but they are also found in Guerrero, Oaxaca, Chiapas, and Guatemala. Accordingly, most of the specimens cited by Munz are not true *L. angustifolia*, due to his misconception of this taxon; they resemble ± the *foliosa*- or Veracruz-type. Several other collections, from various places, are transitional between *L. foliosa* and typical *L. hirsuta*. Collections of *L. foliosa* (or *L. angustifolia* sensu Munz) are, for example: *Purpus 7076*, *Bilimek 961 p.p.*, *Muller (1524)*, *Bourgeau 3226*, *Miranda 650*, *4882*, *Gómez Pompa 1824*, from Veracruz; *Conzatti 4858*, *Galeotti 3060*, from Oaxaca; *Tillett 638–80*, from Chiapas; *Pittier 20*, from Guatemala. Partly so are: *Schiede & Deepe 535*, *Rose & Hay 6148*, *Pringle 8127*, *Seaton 132*, *Balls 4278*, *Conzatti & Gonzáles 1115*, *White 5058*, *Fisher 342*, *C. L. Smith 1786*.

On the other hand certain specimens are intermediate between the true, typical *L. angustifolia* and *L. racemosa* s. str. usually with small capsules; among them: *Palmer 256 1/2 p.p*, *Rzedowski 8110*, from San Luis Potosí; *Palmer 839*, *Ripley & Barneby 13503*, from Durango; *Ripley & Barneby 13365*, from Guanajuato; *L. parvula* (*Nelson 4987*, from Durango) and *L. lineata* (cultivated, *e.g. Raven 11404*) as well as certain collections from Hidalgo might be partly included in this category.

The four species recognized by Munz (1961) and discussed above thus not only intergrade extensively, but they represent particular combinations of characteristics not necessarily representative of entire populations. Furthermore, there are a number of other morphological types within the subspecies that might equally warrant taxonomic recognition, if there were any indication that such recognition would be an aid to understanding the extremely complex pattern of variability in this extraordinary taxon. Among these extreme types are the following:

1. Shrubby plants with leaves partly opposite or clustered; sepals or petals long; anther ca. 2 mm long; petals not auricled; capsules rather large: El Salvador, Volcán San Salvador, *Williams & Molina 15103* (GH); Guatemala, mts. near Hacienda of Chaucol, *E. W. Nelson 3659* (GH, US). A rather similar plant with

proportionally wide and shallowly serrate leaves and claws of upper petals long-ciliate is *Williams, Molina & Williams 25341* (DS) from Lake Atitlán, Guatemala.

2. Branched annuals; racemes long and many-fruited; flowers small and short-pedicelled; lower petals relatively narrow; capsule minute, 2.5–3.5 mm long: Durango, *Palmer 839* (BM, GH, K, MICH, MO, NY, S, UC, US). Somewhat similar plants, with oblong-lanceolate to lanceolate-linear early deciduous leaves and narrow pale-bright petals, have been seen from 19 mi. SW of Durango, *Ripley & Barneby 13503* (DS, NY).

3. Capsules obpyriform, constricted at base; seeds oblong-ovoid: Michoacán, Coalcomán, Sierra Torrecillas, *Hinton et al. 15264 p.p.* (G, GH, MICH, NY, UC). Other collections with such capsules are *Orcutt (4253)* in 3.10.1910, from Xochimilco, Distrito Federal (BM, MO), *Smyth 205* from San Angel, Distrito Federal (US), *Muller 1573* from Vera Cruz to Orizaba (K), and *Rzedowski 23560* from S of Amojileca, Guerrero (IPN).

4. Delicate perennials (or annuals); stems appressed-pubescent, upper leaves somewhat so; leaves narrower than 1.1 cm, remotely or shallowly serrate to almost entire; flowers small; petals subequal (!), 1.2–2 mm wide, oblong-oblanceolate to oblong-obovate, slightly denticulate-sinuate at apex, the upper obtusely and shortly auricled with a single kidney-shaped (!) gland; capsules 2–4 mm in diameter: Chihuahua, W side of sierras, near San Francisco del Oro, *Soderstrom 875* (MICH, US). These plants, out of the range of *L. racemosa* and with habitus and colors of *L. miniata*, might be either intergrades with the latter or an undescribed species.

5. Tiny plants, up to 9 cm tall; leaves to 1.2×0.6 cm, oblong-ovate to lanceolate-linear, remotely serrulate, alternate to opposite; branches and racemes very short; flowers minute, all parts shorter than 3 mm (!); petals hardly clawed, the upper without auricles or distinct glands: Hidalgo, Cerro Cangando, Encarnación, *Paray 3203* (IPN). These plants might be hybrid-segregates or ecotypes or even new species. There are many other small specimens (*e.g. Moore 1565* (BM, GH, MICH, UC) from Pachuca to Real del Monte, Hidalgo, with small, short-pedicelled capsules; *Dugés 308b* (GH) from Santa Rosa Mts. in Guanajuato, with simple stems and small capsules; *Rzedowski 19272* (IPN, MICH) from Ixtlán de Juárez, NE of Oaxaca, with capsules sometimes ellipsoid; *Beauchamp* in October 1926 (MO), from Amecameca, Mexico, with opposite leaves; *Coulter 179* (GH, K, NY) from Zimapan partly so; and likewise from Veracruz, Aguascalientes, San Luis Potosí and Michoacán) yet none is as unique as the ones mentioned above.

6. Generally like "*L. coronata*"; stems angular, slightly winged; leaves acutely serrate; racemes short and crowded; upper petals with a broad constricted or kidney-shaped gland; Nuevo León, Monterrey, canyon above El Diento, *R. F. Smith M575* (TEX). This plant shares some features with *L. nuevo-leonis*. Other specimens ± resembling this one, particularly in having this kind of gland, are recorded from Morelos, Lagunas de Zempoala, *Breedlove 15835* (DS), San Luis Potosí, Sierra de Álvarez, near Puerto Huerta, *Rzedowski 5269* (IPN), Guerrero, México, Oaxaca, Veracruz and Aguascalientes.

Some specimens of *L. racemosa* subsp. *racemosa* have certain features of *L. miniata* subsp. *miniata*, probably the result of convergent evolution rather than hybridization. Such plants have an unusually broad gland on the upper petal, sometimes with small auricles, mostly with small capsules, with long and branched inflorescence and sometimes with shallowly serrulate leaves (*e.g. Ch. L. Smith 844 p.p.* from Oaxaca; *McVaugh & Koelz 153* from Aguascalientes; *Langman 3057* from Michoacán, with small auricles and small glands). These species can be hybridized in the experimental garden, and *Rzedowski 8310* and *10001* might represent wild hybrids of this parentage.

14b. **Lopezia racemosa** subsp. **moelchenensis** Plitmann, Breedlove & Raven, subsp. nov.—Figs. 76–79.

Herbae perennes subglabrae. *Caules* decumbentes ad erectae, strigulosae vel subglabrae, adnodos radicantes. *Folia* crassa, glabra, 0.7–4.4 cm longa, (0.1–)0.2–1.4 cm lata, anguste lanceolata vel rariore ovata vel oblanceolata, serrulata vel serrata. *Petala* carneo-aurantiaca ad rubra. *Pollen* saepe 4-porata interdum 3- vel 5-porata. Numerus chromosomaticus gameticus, $n = 20$.

Subglabrous perennial *herbs*. *Stems* mostly decumbent, sometimes erect, sparsely strigulose, or glabrous rooting at nodes. *Leaves* fleshy, glabrous, 0.7–4.4 cm long, (0.1–)0.2–1.4 cm wide, narrowly lanceolate, more rarely ovate or oblanceolate, acuminate or cuneate-angustate at base, serrulate or serrate, the teeth usually with dark clusters of "oil cells" (Stein, 1915) at the tips. *Pedicels* 1–3 cm long. *Petals* pink-orange to orange-red, sometimes pink-brown or tinged with lilac. *Pollen* with a high proportion of 4-porate and some 5-porate grains, in addition to the 3-porate ones typical of diploids. Gametic chromosome number, $n = 20$.

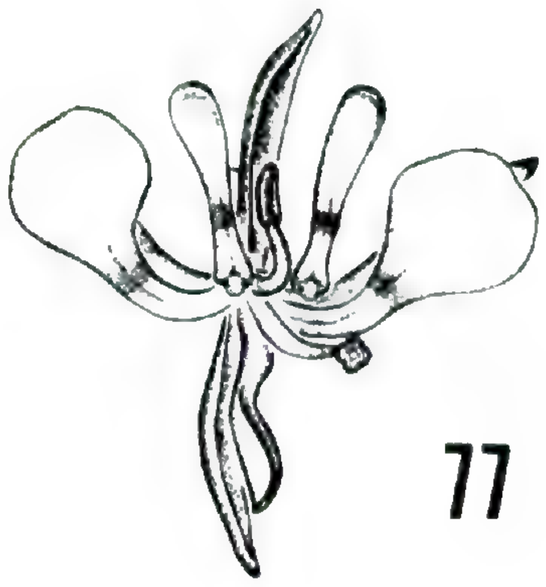
Type: Chiapas, Moel Ch'en near Tenejapa Center, Municipio of Tenejapa, 7500 feet, 30 November 1964, *D. E. Breedlove 7794* (DS).

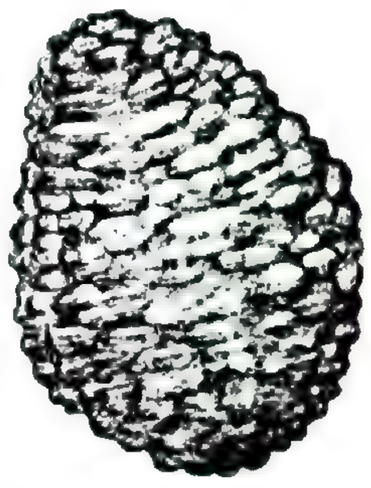
Distribution (Fig. 66): Steep exposed limestone slopes with *Saurauia*, *Quercus*, and *Pinus* in Chiapas, Mexico, and probably northwestern Guatemala, 1800–2500 m elevation. Flowering, November to March but sporadically throughout the year.

Additional specimens examined:

Mexico. chiapas: Chihk Ha', paraje of Yashanal, Tenejapa, *Breedlove 9373* (DS); near Tenejapa Center, *Breedlove 6971* (DS); Moel Ch'en near Tenejapa Center, *Breedlove 9343* (DS).

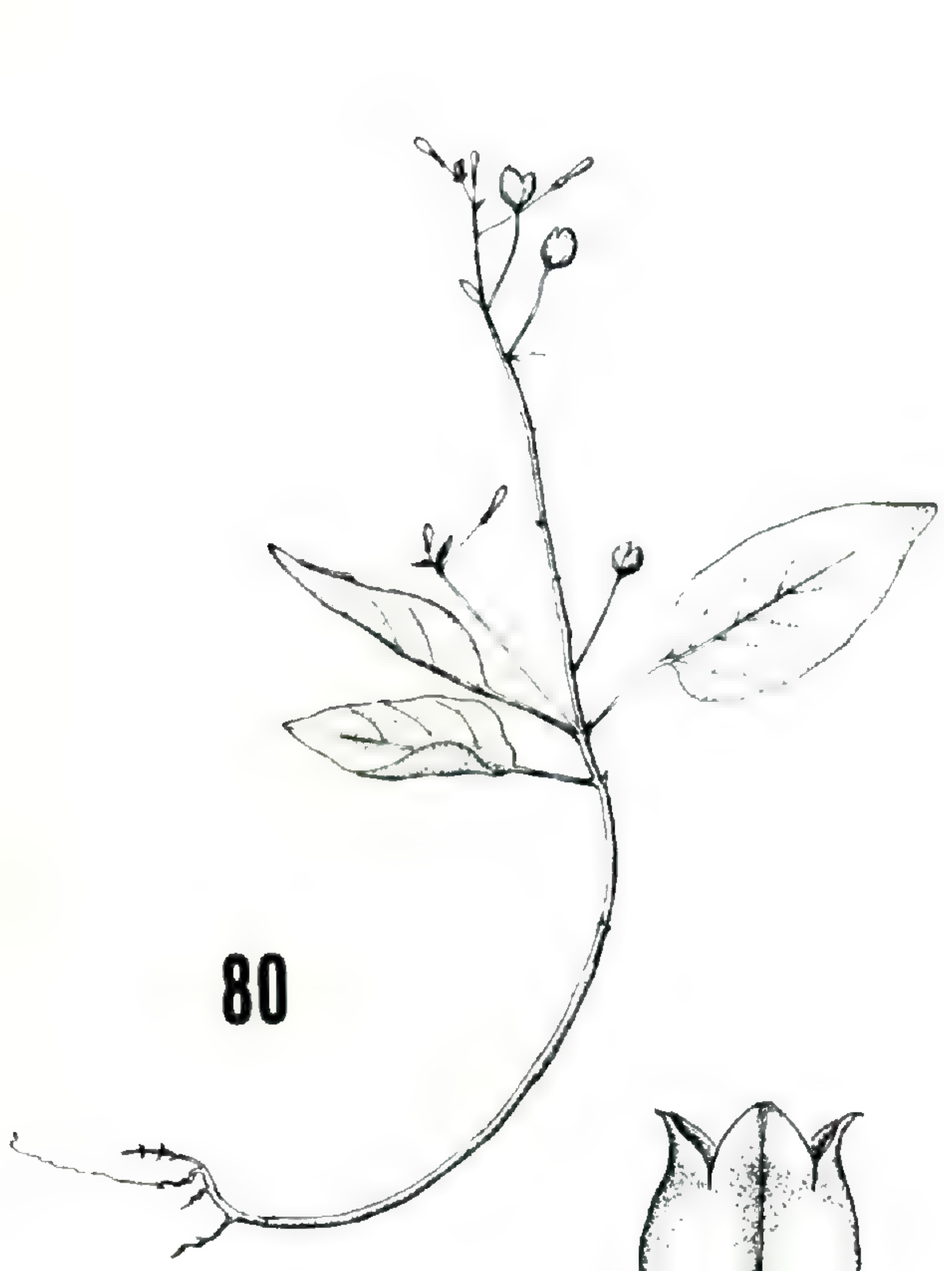
As stressed above, *Lopezia racemosa* subsp. *moelchenensis* is undoubtedly a tetraploid derivative of *L. racemosa* subsp. *racemosa*. Its variability is rather narrow and the various populations are more or less uniform morphologically. It grows exclusively in particular extreme microhabitats under conditions probably unfavorable for the sympatric subsp. *racemosa*. There are important biological distinctions between the two in chromosome number (which leads to a reduction in fertility of the hybrids), ecology, and flowering time (subsp. *moelchenensis* flowers later in the year than subsp. *racemosa*, although sporadically at other times also). These seem to have allowed the evolution of this narrowly restricted but distinctive entity, which might be regarded as a species "in statu nascendi."

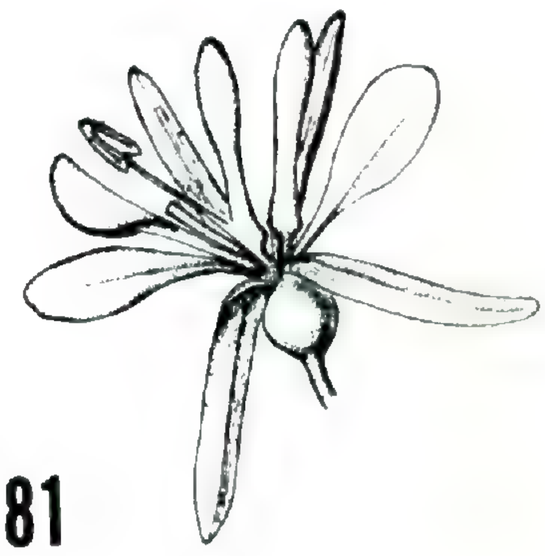


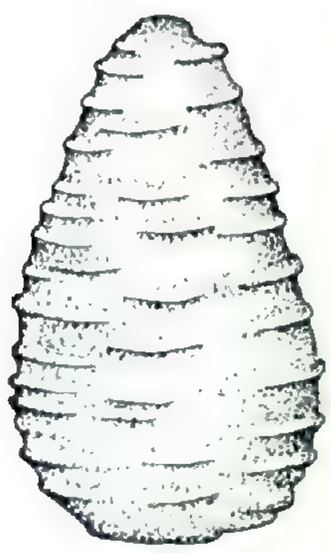


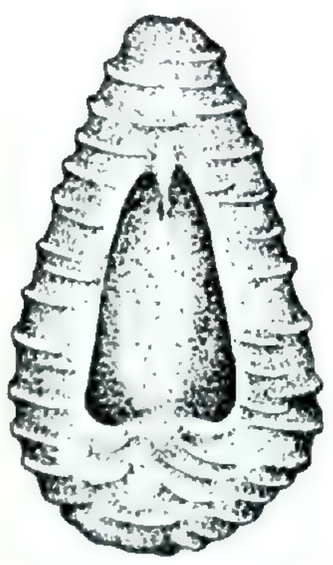
FIGURES 76–79. *Lopezia racemosa* subsp. *moelchenensis*.—76. Branch, × 0.59.—77. Flower, × 2.3.—78. Capsule, × 7.—79. Seed, abaxial view, × 23. All from progeny of the type collection, grown at Stanford University.

A peculiar single collection similar to *L. racemosa* subsp. *moelchenensis* is *Breedlove* 8688 (DS) from stony ledges of the Wahshaklahung Pyramid in San Mateo Ixtatán, Guatemala. The leaves of these plants, which likewise have a gametic chromosome number of $n = 20$, are less fleshy, generally wider and more sparsely hirsute than in subsp. *moelchenensis* from Chiapas; the petioles average longer (to 2 cm); the pedicels ± puberulent-glandular; the petals a little larger; and the pollen grains mostly 3-porate. Plants of this sort have been found only in the Sierra de los Cuchumatanes and might constitute an independent tetraploid derivative of *L. racemosa* subsp. *racemosa* which needs to be studied further in the field. Another collection from the same area, *Breedlove 8496* from 7 mi. S of San Juan Ixcoy along road to Huehuetenango, resembles both the collection from San Mateo Ixtatán and *L. racemosa* subsp. *racemosa* (larger somewhat pubescent leaves, long petioles, large flowers, ± erect stems, etc.).









FIGURES 80–85. *Lopezia conjugens*.—80. Habit, 0.55.—81. Flower, × 2.8.—82. Upper petal, × 3.3.—83. Capsule, × 3.3.—84. Seed, abaxial view, × 22.—85. Seed, adaxial view, × 22. All from the holotype.

15. **Lopezia conjugens** T. S. Brandegee, Univ. Calif. Pub. Bot. 6: 59. 1914. Munz, Brittonia 13: 86. 1961; N. Amer. Fl. II. 5: 21. 1965.—FIGS. 80–85.

Sparsely puberulent or subglabrous *annuals*. Stems 1–3.5 dm tall. *Leaves* 1–4.5(–5) cm long and (0.6–)1–3 cm wide, apparently mostly opposite, ovate, obtuse at base, acute at apex, thin, subglabrous, with 4–8 veins on each side of midrib, shallowly serrulate-crenulate to mostly subentire, remotely ciliolate-strigose; petioles 0.5–3 cm long, slender, usually narrowly winged. *Bracts* 2–10 mm long and 1–2 mm wide, mostly glabrous but slightly hairy toward apex; pedicels 8–17 mm long, spreading to ascending, minutely glandular-puberulent. *Sepals* ca. 5.5–7 mm long and 1–1.5 mm wide, oblong, subglabrous. *Lower petals* ca. 6–7 mm long and ca. 2 mm wide, obovate-spatulate or elliptic-ovate, angustate then clawed at base, obtuse at apex, purplish; upper petals ca. 6 mm long and ca. 1.5 mm wide, oblanceolate-oblong to linear, angustate into a short claw, without a conspicuous gland, obtuse at apex, pale-purplish. *Fertile stamen* ca. 5 mm long; anther ca. 1.5 mm long, purplish. *Staminode* ca. 6 mm long and ca. 3 mm wide, obovate-spatulate, narrowed at base, emarginate at apex, pale purplish. Style ca. 3–4.5 mm long; stigma minute. *Capsule* ca. 5 mm long and 4 mm wide, subglobose, slightly clavate-cuneate at base, glabrous. *Seeds* 1.2–1.5

mm long, oblong-ovoid, somewhat incurved, rugose with linear transverse tubercles, blackish-brown.

TYPE: Mexico, Sinaloa, Copradia (Cofradia), near Culiacán, 25 October 1904, *T. S. Brandegee* (UC; isotype, GH).

Distribution (Fig. 66): A rare endemic of Sinaloa, Mexico. The type locality is now under water.

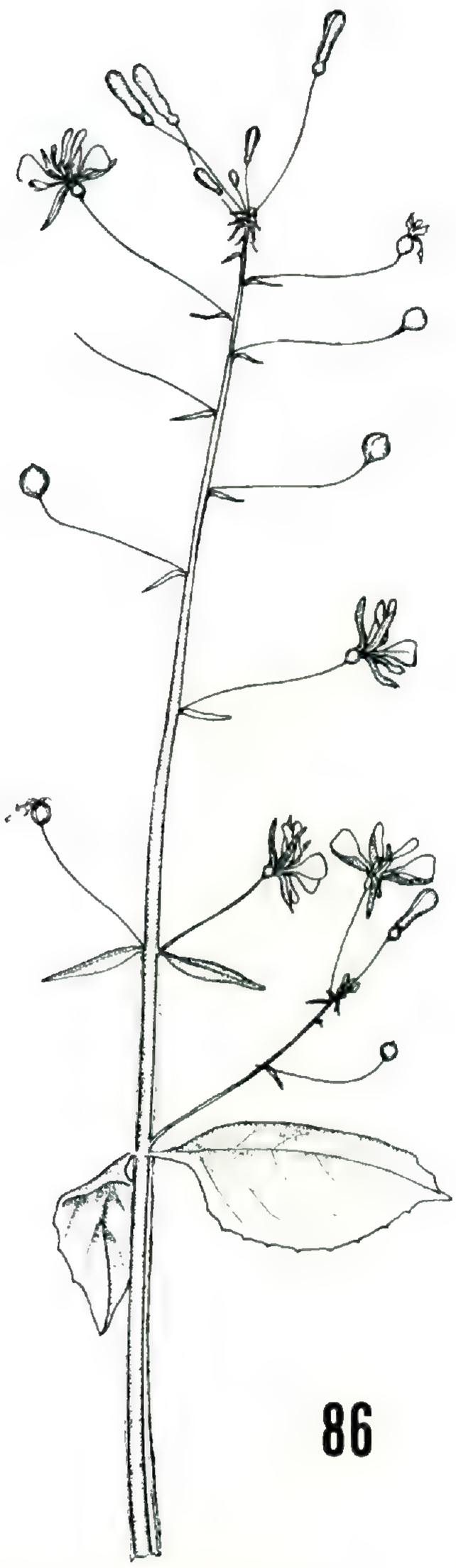
Like *Lopezia smithii*, the following species, *L. conjugens* seems to be an annual derivative of *L. racemosa*, which originated at the margin of distribution of the latter. It is known only from the type collection, which has few flowers and no ecological information.

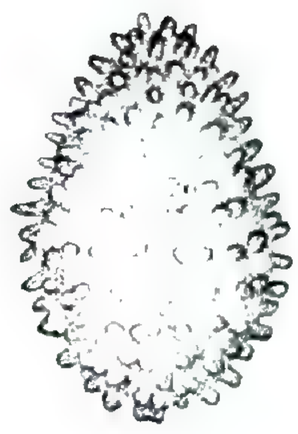
Superficially *Lopezia conjugens* is very similar to *L. racemosa* but distinguished by certain significant traits: Leaves generally opposite, few-veined, shallowly serrulate to subentire; petioles usually narrowly winged; upper petals without a conspicuous gland; anther purple; seeds rugose with linear transverse tubercles, 1.2–1.5 mm long. Brandegee's diagnosis is somewhat inaccurate in a few details: "Petalis superioris—margine infra medium plus minus glandulosis" already emended by Munz as "without conspicuous gland or turbercle"; "inferioribus late linearibus"—whereas they are actually elliptic- or spatulate-obovate. Perhaps Brandegee misinterpreted the position of the flower, viewing the lower petals as upper ones and *vice versa*. In addition, the staminode is *not* minutely serrate; style and filament are a little *shorter* than petals, etc. Munz (1961: 86) described the capsule of *L. conjugens* as slightly clavate at base and uses this character in his key. Considering the wide variation of capsule-shape in *L. racemosa*, and since the clavation in *L. conjugens* is inconstant and slight, this character is not a useful one for separating them.

Brandegee considered *L. conjugens* "intermediate between *Lopezia* proper and *L. clavata*," probably because of his misconception of the petal-position.

16. **Lopezia smithii** Rose, Contr. U. S. Natl. Herb. 12: 300, *fig. 46*. 1909. Munz, Brittonia 12: 85. 1961; N. Amer. Fl. II. 5: 21. 1965.—FIGS. 86–88.

Puberulent-strigose *annuals*. *Stems* 1–7 dm tall, angular and somewhat winged. *Leaves* ovate to lanceolate, the lower to 7 cm long and 2.8 cm wide, the upper 1–3.5 cm long and 0.3–1.5 cm wide, ± cuneate at base with lower part gradually narrowed and somewhat constricted then with usually subparallel sides toward the base, acute at apex, shallowly serrulate, sparsely strigulose, with 5–12 veins on each side of midrib, subsessile. *Bracts* mostly 2–10 mm long and 0.5–4 mm wide, pedicels 10–19 mm long, patent to ascending, sparsely strigulose or puberulent to subglabrous. Sepals ca. 4 mm long and to 1 mm wide; sparsely strigulose or subglabrous. *Petals* pink-lilac to purplish-red; lower petals ca. 6 mm long and 2.5 mm wide, obovate, tapering at base into a claw as long or a little longer than blade, subentire and ± retuse at apex; upper petals ca. 5 mm long and 1 mm wide, linear-oblong, not auricled, with claw shorter than blade and a single yellowish gland at base of blade fringed with marginal short, clavate hairs, retuse to obtuse at apex. *Fertile stamen* ca. 3–3.5 mm long; anther 1–1.5 mm long. *Staminode* 3–4 mm long, obovate, purplish, ± emarginate at apex,





FIGURES 86–88. *Lopezia smithii*.—86. Inflorescence, × 0.58.—87. Flower, × 7.—88. Seed, abaxial view, × 23. All from the holotype.

narrowed into a somewhat dilated and slightly ciliate-pubescent claw. *Style* 2.5–3.5 mm long, thin; stigma minute. *Capsule* 3–4.5 mm long, 2.5–3.5 mm thick, globose, rarely ellipsoid, open a third of its length, glabrous. *Seeds* ca. 1 mm long, oblong-ovoid, muricately and coarsely papillose-tubercled, brown.

TYPE: Mexico, Oaxaca, Jayacatlán, 4300 feet, 4 November 1895, *C. L. Smith 294* (US; isotype, GH).

Distribution (Fig. 66): Endemic in the mountains at the northeast end of the valley of Oaxaca, Mexico. Flowering, November and December.

Additional specimens examined:
MEXICO. OAXACA: Mountains, San Juan del Estado, *C. L. Smith 427* (GH, US).

Collected only twice, by C. L. Smith, from neighboring localities, *Lopezia smithii* is probably an annual derivative of *L. racemosa*. Unfortunately, nothing is known about its habitat or its chromosome number. This species is easily distinguished by its slightly winged stems, subsessile leaves with unique base, ± retuse petals, and the clavate hairs at base of the upper petals and around the glands. In other respects, its resembles *L. racemosa*.

Section V. **Nannolopezia**

Lopezia sect. *Nannolopezia* Plitmann, Raven & Breedlove, sect. nov.

Herbae tenues annuae. *Folia* alternantia, integra. *Inflorescentia* terminalia, racemosa. *Flores* purpurei albique, autogami, partibus libris. *Sepala* subaequalia. *Petala* alba, superiora quam inferiores angustiora, 1-glandulosa. *Stamen inferiorum* infertilis; stamen superiorum tortum vel intortum. *Pollen* caeruleum. *Capsula* subglobosa. *Semina* 4, tuberculata, papillis parvibus longitudinalibus. Numerus chromosomaticus gameticus, $n = 7$.

Slender stemmed annual *herbs*. *Leaves* alternate, entire. *Inflorescence* terminal, racemose. *Flowers* purplish and white, autogamous, the parts free. *Sepals* subequal, often reddish. *Petals* white, the upper ones somewhat narrower than the lower ones, 1-glanded. *Upper stamen* fertile, the lower one petaloid but not clasping the fertile one; upper end of filament of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position, or not, in any case shedding pollen directly upon the simultaneously maturing stigma. *Pollen* blue. *Capsule* small, subglobose, the valves splitting for about a third of their length. *Seeds* one per locule, longitudinally papillose-tuberculate. Gametic chromosome number, $n = 7$.

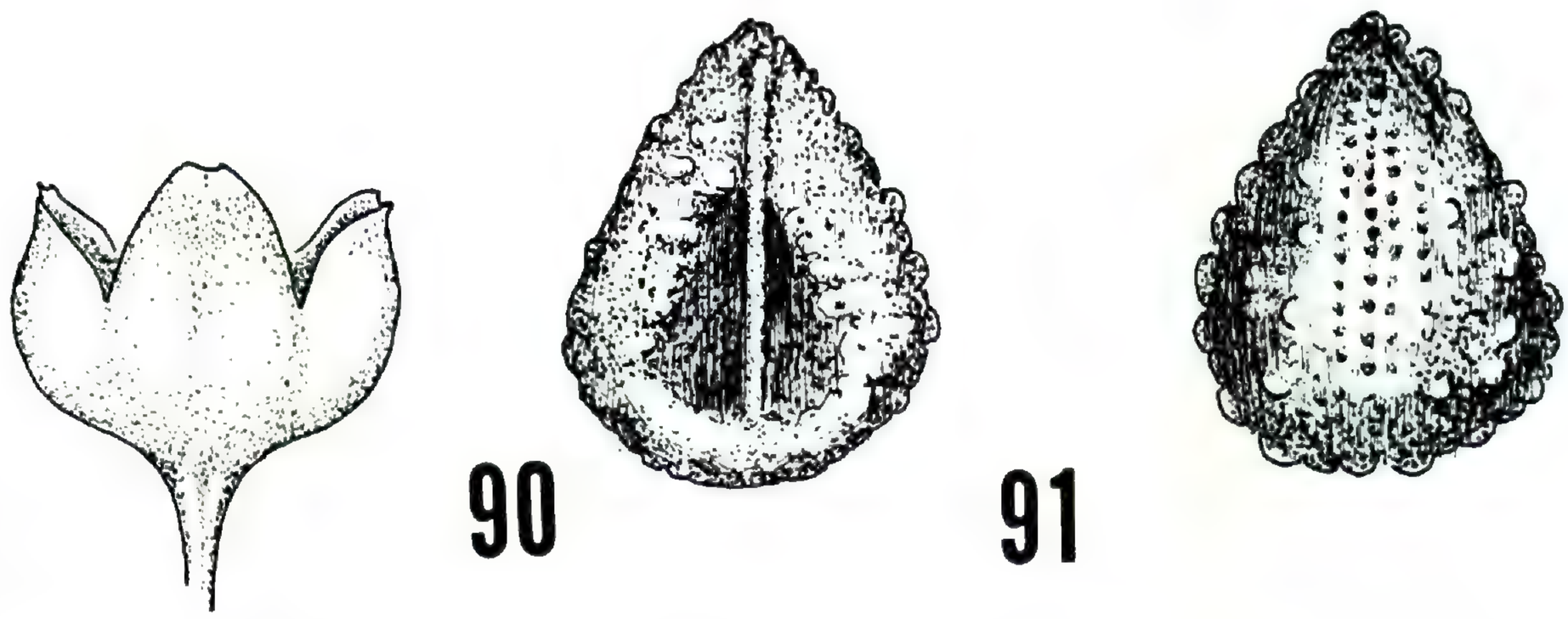
TYPE SPECIES: *Lopezia gracilis* S. Wats.

Distribution: Pine-oak forests of the Sierra Madre Occidental of Sonora, Chihuahua, and northern Durango, Mexico, 1700–2700(–3000) m elevation.

For a time, we considered this morphologically and chromosomally distinct species as a probable derivative of sect. *Lopezia*; there is, however, no evidence that it was in fact derived from a species in which the snapping mechanism of the fertile anther and staminode was present, especially in view of the somewhat distinctive anatomical features discussed by Eyde and Morgan (1973). We now regard it as derived from the ancestors of the evolutionary line that later gave rise to sect. *Pelozia*, but before the fusion of floral parts that is characteristic of this line had appeared.

17. **Lopezia gracilis** S. Wats., Proc. Amer. Acad. Arts 21: 429. 1886. Munz, Brittonia 13: 84. 1961; N. Amer. Fl. II. 5: 20. 1965.—FIGS. 89–91.

Delicate subglabrous *annuals*. *Stems* 1–3.5 dm tall, ascending to erect, usually branched, thin and slender, terete. *Leaves* 0.4–2.9 cm long and 0.1–1 cm wide, broadly lanceolate or oblanceolate to linear, usually narrow, obtuse to cuneate at base, subacute at apex, entire; petioles 0–0.8 cm long. *Bracts* narrow, linear to filiform; pedicels 7–15 mm long, ascending or spreading. *Sepals* 2–4 mm long and ca. 1 mm wide, glabrous. *Lower petals* (2.5–)3–4.5 mm long and 2–3 mm wide, obovate-suborbicular, obtuse, angustate then short-clawed, white; upper petals (2.5–)3–5 mm long and 1.2–2.2 mm wide, oblong, subacute to obtuse, obtuse-



FIGURES 89–91. *Lopezia gracilis*.—89. Capsule, × 11.—90. Seed, adaxial view, × 36.—91. Seed, abaxial view, × 36. All from *Gentry* 635 (DS).

truncate to subcordate at base of blade, short-clawed, white with a broad green gland and a red blotch or band above it. *Fertile stamen* ca. 2.5 mm long; anther ca. 0.7 mm long. *Staminode* 2–3 mm long, obovate-obcordate, angustate-clawed below blade but a little dilated (like filament) at base, white. *Style* 2–3 mm long; stigma 0.5–0.7 mm in diameter, white; ovary obovoid-subglobose. *Capsule* 1.5–3 mm long, 1.5–3 mm thick, subglobose, subangular; valves ovate, somewhat wrinkled, ± recurved and sometimes dark at the slightly emarginate apex. *Seeds* 1–1.5 mm long, ca. 0.8 mm thick, ovoid or obovoid, longitudinally papillate-tuberculate, dark brown. Gametic chromosome number, $n = 7$.

TYPE: Mexico, Chihuahua, Cumbre, above Batopilas, October 1885, *E. Palmer 337* (GH; isotypes, BM, MEXU, NY, US).

Distribution (Fig. 34): Sandy creek banks and open places in pine-oak forests of the Sierra Madre Occidental of Sonora, Sinaloa, Chihuahua, and northernmost Durango, Mexico, 1700–2700(–3000) m elevation. Flowering, August to October.

Representative specimens examined:

MEXICO. SONORA: El Campanera, 41 mi. NE of Nuri, *Dunn 9101* (RSA); El Rancho del Roble, NE of El Tigre, *White 4314* (MICH); El Bilito, NE of El Tigre, *White 4779* (GH, MICH); Cananea, Municipio de Yecora, *Donnelly 48* (UC); El Tigre Canyon, E of Esqueda and Lago Angostura, *Turner et al. 2105* (DS, MEXU). CHIHUAHUA: 10 mi. N of Madera along rd to Chuhuichupa, *Breedlove 15535* (DS); Santo Domingo on Matachic-Ocampo, *Hewitt 81* (GH); Cañon Huahuatán, SE of Madera, *Müller 3442* (GH, US); Sierra Madre, SE of Colonia Garcia, *Townsend & Barber 281* (BM, G, GH, K, MO, NY, P, US, Z); Sierra de las Papas, *Gentry 635M* (DS, MICH); Memelichi, Río Mayo, *Gentry 2749* (GH, MEXU, MO, S, UC, US); Sierra Gazachic, 35 km SW of Miñaca, *Pennell 18880* (MEXU, NY, US); base of Cerro Mohinora, 8 mi. from Guadalupe y Calvo, *Nelson 4834* (GH, US), *Pennell 18976* (US). SINALOA: 5 mi. E of La Cienega, Sierra Surutato, *Breedlove & Thorne 18563* (CAS, DS, RSA). DURANGO: Hidalgo del Parral to El Vergel, 11.5 mi. W of Ojito, *Reveal & Hess 3034* (US).

Sereno Watson (1886: 429) accurately listed the main distinctions between *Lopezia gracilis* and *L. cornuta*. These species occur sympatrically in the southern parts of the range of *L. gracilis*, but *L. cornuta* apparently grows in moister places. These two species show homologous variability in many traits. *Lopezia gracilis* has small white flowers and is highly self-pollinated; insects very rarely visit its flowers. Its stamen is not always completely twisted, and it can shed the pollen on the stigma just below it.

Section VI. **Pelozia**

Lopezia sect. *Pelozia* (Rose) Plitmann, Raven & Breedlove, comb. nov.

Pelozia Rose, Contr. U. S. Natl. Herb. 12: 295. 1909.

Well branched annual *herbs or* stoloniferous *perennials*. *Stems* often reddish. *Leaves* alternate. *Inflorescence* terminal, racemose, leafy, often reddish. *Flowers* pinkish or lilac to red or purplish, often with white markings, extremely zygomorphic, protandrous or autogamous, the constriction separating perianth, style, and androecium from the ovary prolonged into a neck. *Flower* parts except the staminode and lower sepal greatly displaced to upper side of flower, the three upper sepals and two upper petals united near the base, with the median upper sepal bearing a prominent gland at approximately the level of divergence and the two upper petals bearing less prominent or obsolete glands at this level; upper petals ± equal to or much larger than the lower ones. *Sepals* often reddish. *Style* and *fertile stamen* united to one another and to the other upper floral parts near the base, but diverging well below the level of separation of the upper petals; upper stamen fertile, the lower one petaloid but not clasping the fertile one; upper end of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. In protandrous species, fertile stamen reflexes downward after shedding its pollen while style elongates to occupy its former position. *Pollen* blue or yellow. *Capsule* ovoid to subglobose or clavate-obconical or subcylindrical, widely open at maturity or the valves opening at the very apex only, often reddish. *Seeds* many, small, finely tuberculate. Gametic chromosome numbers, $n = 10, 9, 7$.

Type species: *Lopezia laciniata* (Rose) M. E. Jones.

Distribution: Mexico, from southern Baja California and Sinaloa south in the Sierra Madre Occidental to Durango and Jalisco, in oak-pine forest or subtropical thorn shrub, 100–2000 m elevation.

18. **Lopezia lanciniata** (Rose) Jones, Contr. West. Bot. 15: 147. 1929. Munz, Brittonia 13: 83. 1961; N. Amer. Fl. II. 5: 20. 1965.

Pelozia laciniata Rose, Contr. U. S. Natl. Herb. 12: 296, *fig.* 38. 1909.

Generally subglabrous perennial *herbs*. Stems 1–6 dm tall, decumbent to erect, hirtellous, especially at base, to subglabrous; branches slender, glabrescent. *Leaves* thick, 0.7–5 cm long and 0.2–2.2 cm wide, the lower ones ovate to oblong or lanceolate, subcordate to obtuse or tapering to cuneate at base, acute or acuminate at apex, remotely serrate or serrulate, sparsely strigulose-hirtellous to subglabrous, upper leaves smaller, oblong to narrowly lanceolate, obtuse to acute-cuneate at base, acute at apex, subserrate to subentire, subglabrous, all with 0–5 veins on each side of midrib; petioles (1–)2–23(–29) mm long, subglabrous. *Bracts* 5–25 mm long and 1–6 mm wide, subglabrous; pedicels 15–45(–50) mm long, ascending to erect, sparingly glandular-puberulent to subglabrous. *Flowers* protandrous. *Sepals* 3.5–7 mm long and 1–1.5 mm wide, a few hairs present at apex, otherwise subglabrous. *Petals* white with red veins; lower petals 4–6.5 mm long and 1.5–2 mm wide, linear-oblong, sessile, subacute

and subentire at apex, sometimes retuse-bidentate, with subentire margins; upper petals 4–6.5 mm long and 3–4.5 mm wide, obovate-obtriangular, bipartite and shortly (3–)4(–5)–laciniate, somewhat clawed, adnate at base to upper sepals ± dentate or incised at apex, sparsely serrate. *Fertile stamen* 3–5 mm long; anther 1–2 mm long, red. *Pollen* blue. *Staminode* 2.5–4.5 mm long, linear, plane or concave, white with red markings. *Style* 3–4.5 mm long; stigma 1–1.5 mm in diameter, whitish or lilac; ovary 1.5–2.5 mm long, obovoid-ellipsoid, ± glandular-puberulent. capsule 2–5 mm long, 2–4 mm thick, obovoid-obconical, cuneate at base, truncate and dentate at apex, puberulent or subglabrous; valves open widely to about a third of their length. *Seeds* 0.5–0.9 mm long, ovoid, somewhat compressed, blackish. Gametic chromosome number, $n = 10$.

Distribution (Fig. 20): Moist seepages, especially along cliffs and in rocky places, in the Sierra Madre Occidental, in Mexico, (800–)1300–2800 m elevation. Flowering, October to February (March).

KEY TO THE SUBSPECIES

Stems short-hirsute; leaves narrowly lanceolate to lanceolate, all narrower than 1 cm, the upper ones very shortly petiolate ..... 18a. subsp. *laciniata*
Stems subglabrous; leaves ovate to lanceolate, some wider than 1 cm, the upper ones distinctly petiolate ..... 18b. subsp. *ovata*

18a. **Lopezia laciniata** subsp. **laciniata**.—FIGS. 92–96.

Stems rigid, ± erect, short-hirsute. *Leaves* relatively narrow (all narrower than 1 cm), lanceolate or narrowly lanceolate, acuminate at base and apex, the upper ones very short-petioled.

TYPE: Mexico, Jalisco, on mountains near Talpa, 4400–5000 feet elevation, 7 March 1897, *E. W. Nelson 4035* (US; isotype, GH).

Distribution (Fig. 20): Moist seeps in the Sierra Madre Occidental of Jalisco, Mexico, 1400–2000 m elevation. Flowering, October to February.

Additional specimens examined:
MEXICO. JALISCO: Sierra de la Campana 7–8 mi. NW of Los Volcanes, *McVaugh 13760* (BM, MEXU, MICH, RSA, US); Hacienda del Ototal, E of San Sebastián, *Mexia 1688* (BH, BM, G, GH, MO, NY, UC, US); Real Alto to Tranquillas, *Mexia 1714* (BM, DS, MICH, US); NNE of Talpa de Allende, *McVaugh 20347* (MICH).

18b. **Lopezia laciniata** subsp. **ovata** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 280. 1973.—FIG. 97.

Stems flexible, creeping to ascending, sometimes very slender, subglabrous. *Leaves* ovate to lanceolate, some wider than 1 cm and occasionally to 2.2 cm, subcordate to subacute at base, acute at apex, the upper ones distinctly petioled. Gametic chromosome number, n = 10.

Type: Mexico, Durango, 20 mi. W of La Ciudad, steep moist cliff on edge of barranca, 7600 feet, 3 October 1966, *D. E. Breedlove 15552* (DS, holotype).

Distribution (Fig. 20): Moist places, usually on wet cliffs and slopes, in rock crevices or near streams, Sierra Madre Occidental of Durango and Sinaloa, Mexico, (800–)1300–2800 m elevation. Flowering, October to February (or March).

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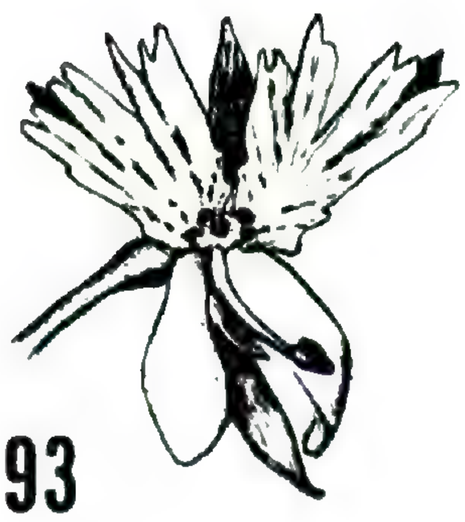

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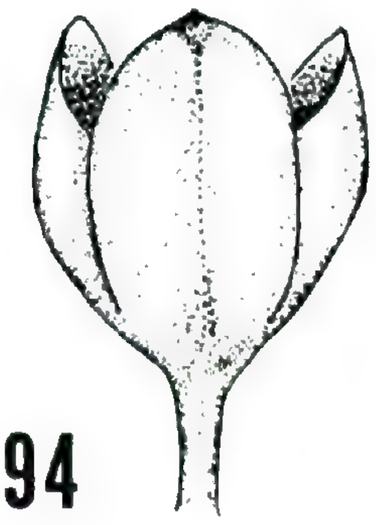

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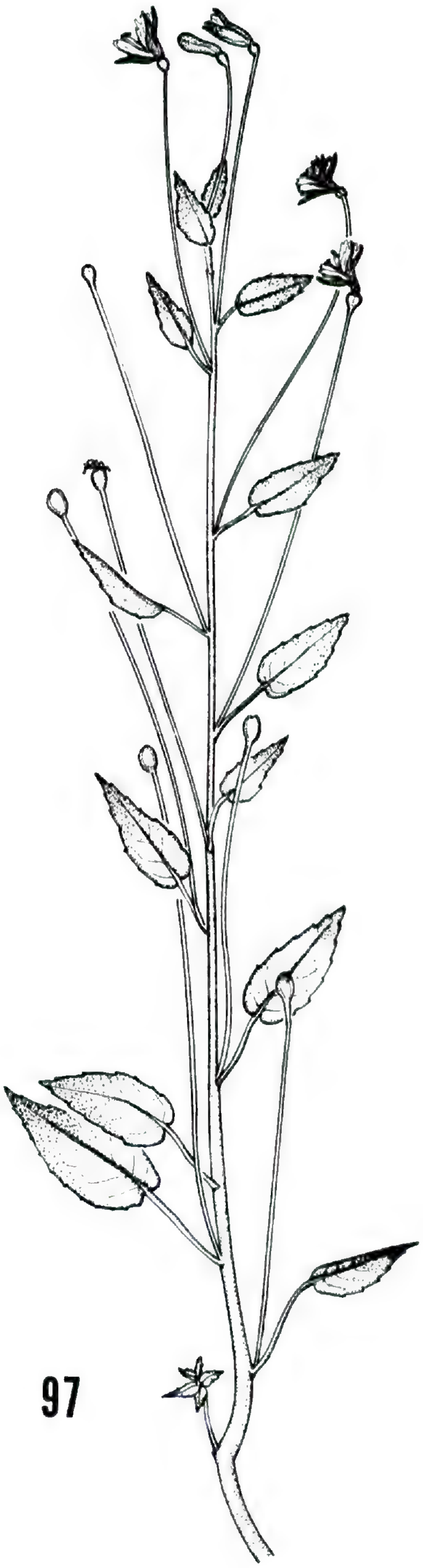

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Representative specimens examined:

MEXICO. SINALOA: 1 mi. W of El Palmito, ca. 45 mi. E of Concordia, Rosario, *Breedlove 4248* (DS), *Gentry & Arguelles 18197* (pedicels up to 5.5 cm; US); 0.4 mi. E of Portrerillos, ca. 34 mi. E of Concordia on Mexican Hwy. 40, Rosario, *Breedlove 1672* (DS, RSA); Sierra Madre Mts., "El Batel," *Mexia 468* (MO, UC); El Carrizo, *Ortega 6035* (POM, US); 59 mi. E of Villa Union, *Wiggins 13197* (DS). DURANGO: 13 mi. W of La Ciudad, *Breedlove 15548* (DS), *Flyr 285* (TEX); 9 mi. E of El Palmito, 55 mi. E of Concordia, Pueblo Nuevo, *Breedlove 4255* (DS); W slope of Sierra Madre nr El Espinazo, *Ripley & Barneby 14011* (NY); Los Angeles, Sierra Madre Occidental, *Goodman 7418* (DS, RSA, UC); 50 mi. WSW of El Santo, *McVaugh 11589* (MICH).

Particularly in this subspecies, the plants creep and root at the nodes, forming large mats up to several meters across, a habit unique in the genus.

19. **Lopezia gentryi** (Munz) Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—FIGS. 98–101.

Lopezia laciniata (Rose) Jones subsp. *gentryi* Munz, Brittonia 13: 84. 1961. Munz, N. Amer. Fl. II. 5: 20. 1965.

Delicate annual *herbs*, sparsely glandular-puberulent or subglabrous. *Stems* 0.6–2(–2.5) dm tall, thick, slender, decumbent to ascending, sometimes rooting. *Leaves* (0.5–)0.9–2.8 cm long and 0.1–0.7(–1.5) cm wide, narrowly lanceolate or linear, rarely broadly lanceolate, obtuse to angustate at base, ± acute at apex, serrate or serrulate, green to purplish, subglabrous or very sparsely puberulent; petioles short, 0.1–2.2 cm long, slender, narrowly winged or not, subglabrous. *Bracts* 0.5–1.5 mm wide, rarely wider; pedicels 10–35 mm long, spreading to erect. *Flowers* autogamous. *Sepals* (3–)3.5–4(–5) mm long, ca. 1 mm wide, with a few hairs at the acute apex, often reddish. *Petals* white with red veins; lower petals (2.5–)3.5–5(–6) mm long and 1–1.7 mm wide, linear or lanceolate, subsessile or hardly clawed, entire, subacute or obtuse or somewhat retuse and minutely denticulate at apex; upper petals 3.5–5(–6) mm long and 2.5–3.5 mm wide, obovate, ± deeply 2–4-laciniate, narrowed at base but not clawed, cleft and dentate or subentire at apex, the margins sparsely dentate. *Fertile stamen* (2.5–)3–4.5(–5) mm long; anther 0.7–1.5 mm long, red. *Pollen* blue. *Staminode* 2–3 mm long, linear, white to sometimes pinkish. *Style* 3–3.5(–4) mm long; stigma 1–1.7 mm in diameter, whitish. *Capsule* 2–3.5 mm long, 1.7–3(–4) mm thick, subglobose (obpyriform), setose toward tip with few or many hairs, these often tuberculate; valves open widely to about a third of their length. *Seeds* ca. 1 mm long, ovoid, somewhat compressed, dark brown to blackish. Gametic chromosome number, $n = 8, 7$.

TYPE: Mexico, Sinaloa, Ocurahui, Sierra Surutato, 6000–7000 feet elevation, 1–10 September 1941, *H. S. Gentry 6256* (US; isotypes, DS, GH, MO, NY).

Distribution (Fig. 26): Seepages, especially along crevices and ledges, in the Sierra Madre Occidental, Mexico; Sierra Surutato, Sinaloa; along Mexican

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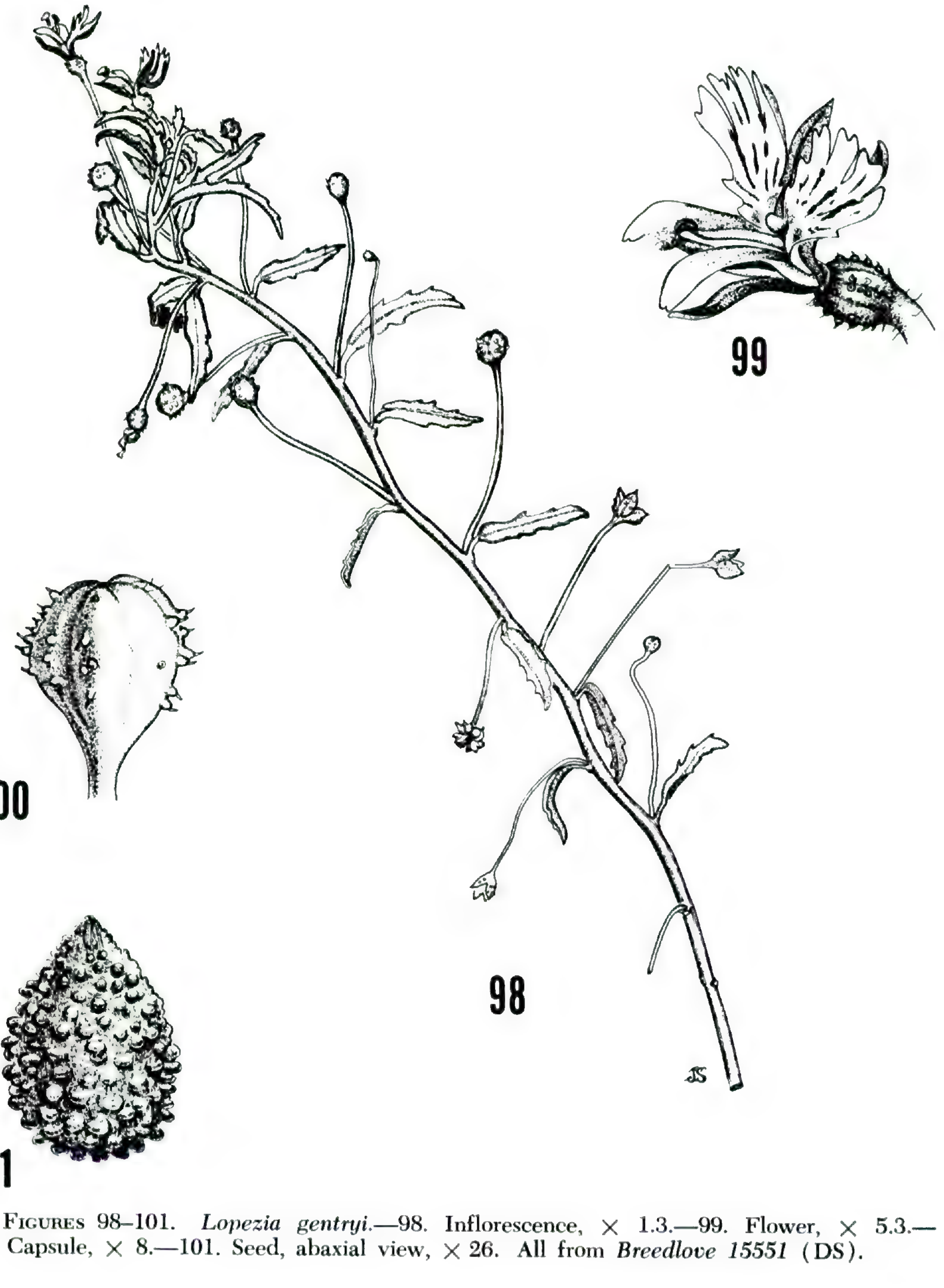
FIGURES 92–97. *Lopezia laciniata*.—92–96. *L. laciniata* subsp. *laciniata*.—92. Branch, × 0.6.—93. Flower, × 3.6.—94. Capsule, × 7.2.—95. Seed, abaxial view, × 24.—96. Seed, adaxial view, × 24.—97. *Lopezia laciniata* subsp. *ovata*, branch, × 1.2.—Figs. 92–93 from *McVaugh 13760* (MICH); Figs. 94–96 from *Mexia 1714* (DS); Fig. 97 from the type collection of subsp. *ovata*.

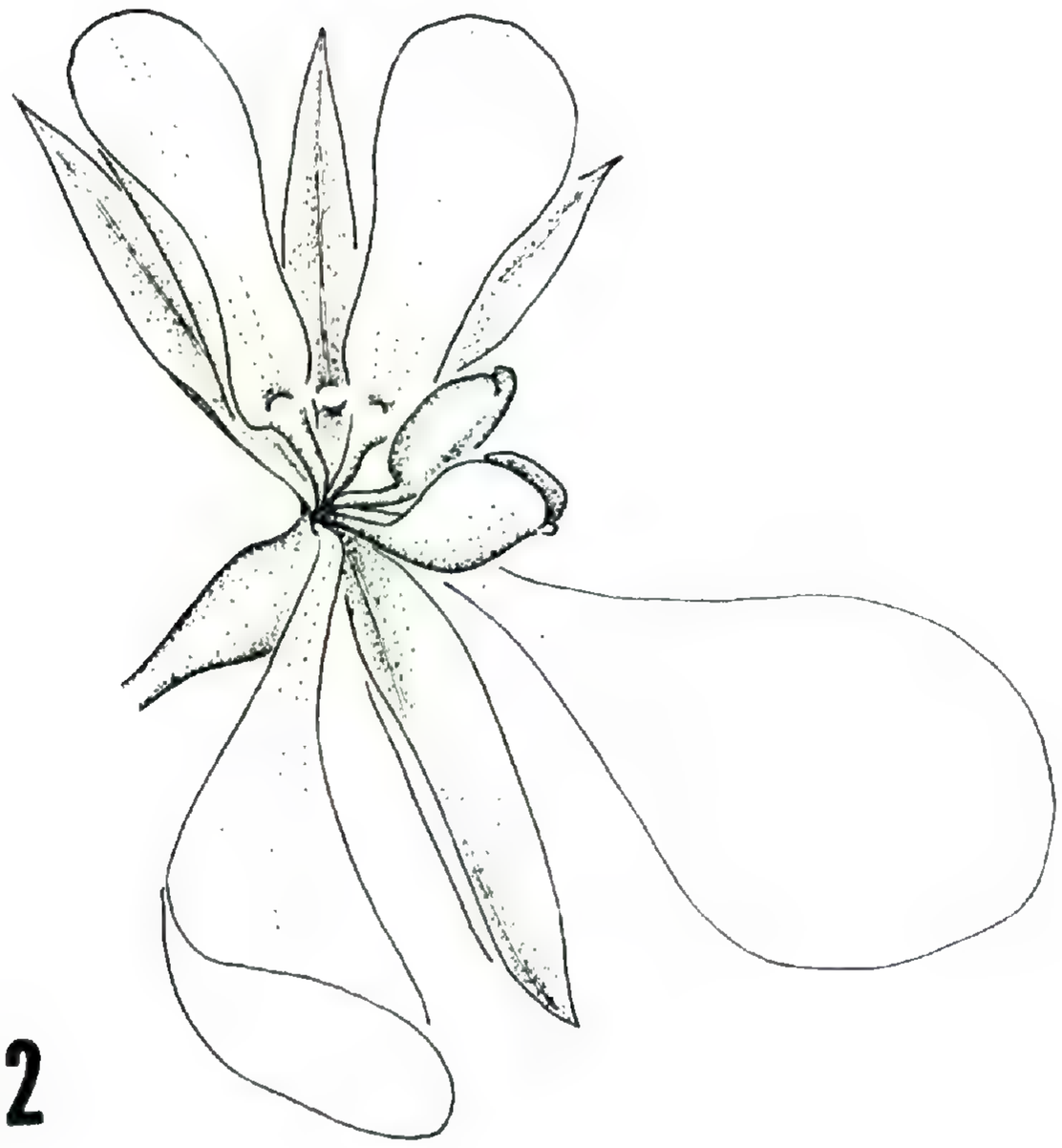


FIGURES 98–101. *Lopezia gentryi*.—98. Inflorescence, × 1.3.—99. Flower, × 5.3.—100. Capsule, × 8.—101. Seed, abaxial view, × 26. All from *Breedlove 15551* (DS).

Highway 40 for about 30 miles, Sinaloa and Durango, 2000–2600 m elevation. Flowering, September and October.

Additional specimens examined:

MEXICO. SINALOA: 3 mi. SE of Los Hornos, Sierra Surutato, *Breedlove & Kawahara 16963* (CAS), *Breedlove & Thorne 18448* (CAS, RSA); 5 mi. NE of La Cienega, Sierra Surutato, *Breedlove & Kawahara 17059* (CAS); 4.4 mi. SW of El Paraíso, Villa Union to El Salto, *Ownbey & Ownbey 1914* (BM, MICH, NY, RSA, UC, US). DURANGO: 17 mi. W of



FIGURES 102–105. *Lopezia clavata*.—102. Flower, × 7.4.—103. Capsule, × 4.4.—104. Seed, abaxial view, × 30.—105. Seed, adaxial view, × 30. All from *Moran 7139* (DS).

La Ciudad, *Breedlove 15551* (DS); 20 mi. W of La Ciudad, *Breedlove 1553* (DS); 16 mi. E of El Palmito, *Breedlove 7231* (DS); 5 mi. W of Revolcaderos, 6800 feet, *Breedlove 15555* (DS).

This species is clearly a reduced, annual, autogamous derivative of *Lopezia laciniata* subsp. *ovata*, smaller in all of its parts, and with reduced gametic chromosome numbers of $n = 8$ and 7 instead of $n = 10$.

20. **Lopezia clavata** T. S. Brandegee, Proc. Calif. Acad. II, 2: 157, *pl. 4*. 1889. Munz, Brittonia 13: 82. 1961; N. Amer. Fl. II. 5: 19. 1965.—FIGS. 102–105.

Pelozia clavata (Brandegee) Rose, Contr. U. S. Natl. Herb. 12: 296, *fig. 37*. 1909.

Glandular-puberulent and sparsely pilose to glabrous annual *herbs*. *Stems* 2–6.5 dm tall, erect; branches glabrous to ± densely pilose with patent short and long hairs. *Leaves* thin, sparsely and ± divaricately pilose or puberulent to glabrous; lower leaves 1.5–8 cm long and 0.7–6 cm wide, ovate to lanceolate, rounded or broadly cuneate and sometimes asymmetrical at base, acute or acuminate at apex, serrate or serrulate, sometimes ciliolate, with 5–10 veins on each side of midrib; upper leaves 0.25–0.7 cm wide, lanceolate, obtuse at base, angustate at apex, subserrate or serrulate; petioles 0.15–3.5 cm long and ca. 0.1 cm wide, slender, patent-pilose to subglabrose, some narrowly winged. *Inflorescences* ± pilose to subglabrous; bracts 3–25 mm long, 1–9 mm wide, glabrous; pedicels 5–27(–35) mm long, ascending to erect, ± pilose to subglabrous. *Flowers* mostly autogamous. *Sepals* 3.5–6 mm long, subglabrous.

Petals pinkish or lilac to sometimes red or purplish; lower petals (3–)5–9 mm long and 2–4.5 mm wide, obovate, clawed-angustate at base, rounded at apex; upper petals (2.5–)4–6 mm long and 0.7–2.5 mm wide, oblong-spatulate, slightly dilate then somewhat clawed at base, obtuse at apex. *Fertile stamen* 1.5–3 mm long; anther 1.5–1.7 mm long, yellowish. *Pollen* yellow. *Staminode* 2–3 mm long and 1–2 mm wide, obovate-spatulate, clawed, retuse at apex, white or reddish. *Style* ca. 2 mm long; stigma 0.5–0.8 cm in diameter, lilac; ovary 1.5 mm long, 0.5–1 mm thick, ellipsoid, ± pilose near tip. *Capsule* (4–)5–10(–13) mm long, 1.2–2.5 mm thick, clavate-obconical or subcylindrical, tapering at base, truncate and dentate at tip, pilose with apical hairs to subglabrous, erect; valves open at summit only as erect or divaricate teeth. *Seeds* 0.5–1 mm long, oblong or ovoid, brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Baja California, Comondú Cañon, base of cliffs, 19 February 1889, *T. S. Brandegee* (UC; isotypes, GH, US).

Distribution (Fig. 34): Near streams or in moist or shaded places, usually on sandy soil, in Baja California Sur, Mexico, from the Sierra de la Giganta to the mountains of the Cape region, and on Isla Partida in the Golfo de California, 100–1800 m elevation. Flowering, October to March.

Representative specimens examined:

MEXICO. BAJA CALIFORNIA: Cape Region Mts., *Brandegee*, 1899 (POM), 1902 (GH, UC, US), *Erabendorffer*, 1891 (UC), *Moran 7139* (DS, IPN), *7090* (DS, IPN), *Thomas 7850* (DS, RSA); Saucito, *Brandegee*, 1893 (UC); Sierra de Laguna, *Brandegee 221* (UC), *Nelson & Goldman 7433* (POM, US), *Hammerly 367* (DS, GH, US), *Carter et al. 2392a* (DS, GH, MO, S, US), *2392* (DS, GH, US); Arroyo Hondo, Sierra Giganta, *Gentry 4123* (DS, GH, MO, UC, US), *Carter et al. 2019* (DS, US); Arroyo Quisapol, E of La Presa, Sierra de la Giganta, *Wiggins 15542* (DS); La Campana, Sierra de las Palmas, *Gentry & Fox 11791* (MEXU); Arroyo de San Bartolo, *Wiggins 14752* (DS, IPN, MEXU, TEX, UC); Arroyo de León, 22 mi. SE of La Paz to Las Planes, *Wiggins et al. 472* (DS, MEXU, UC), *Porter 248* (DS, MEXU); San Bartolo, *Jones 24287* (POM); W shore of Isla Partida, *Wiggins et al. 405* (DS, MEXU, UC); Laguna Mts., *Jones 24153* (DS, MICH, MO, NY, POM, UC, US), *24288* (MICH, MO, NY, POM, UC, US); Todos Santos, *Jones 24286* (POM, US); El Taste ridge, NE of La Carrerita, *Carter & Chisaki 3531, 3574* (both RSA); San José del Cabo, *Jones*, 1928 (POM); S of Miraflores, *Wiggins 14734* (DS); E slope of Cerro Barranco, Sierra Santa Lucia, *Moran 11786* (DS); Arroyo San Martes, 6 mi. SW of Santiago, *Thomas 7721* (DS).

This species is extremely variable in the size and hue of its flowers and in the dimensions of its leaves and capsules.

21. **Lopezia sinaloensis** Munz, Brittonia 13: 83. 1961. Munz, N. Amer. Fl. II. 5: 20. 1965.—FIGS. 106–108.

Densely pilose with patent or retrorse long hairs. *Stems* ca. 3 dm tall. *Leaves* ca. 1–2.5 cm long (or longer?), ovate, obtuse or acute, subentire, the upper smaller, linear; petioles ca. 0.3–1.2 cm long. *Inflorescence* few-flowered. *Pedicels* ca. 20–25 mm long, slender, sigmoid-spreading in fruit. *Flowers* much as in *L. clavata*. *Sepals* ca. 5 mm long. *Petals* pale pink, the lower ones ca. 7 mm long,

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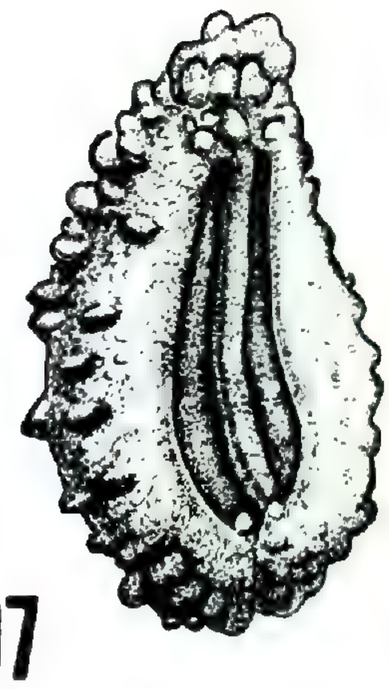
FIGURES 106–108. *Lopezia sinaloensis*.—106. Branch, × 1.2.—107. Seed, adaxial view, × 25.—108. Seed, abaxial view, × 25. All from the holotype.



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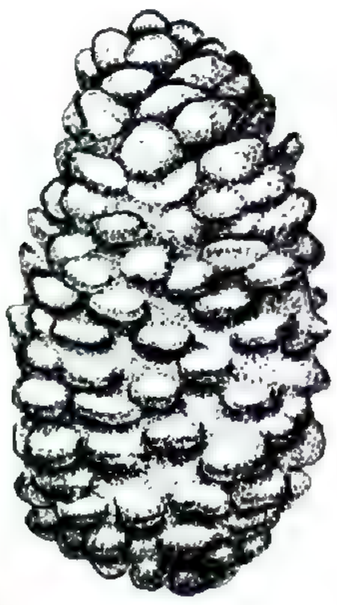

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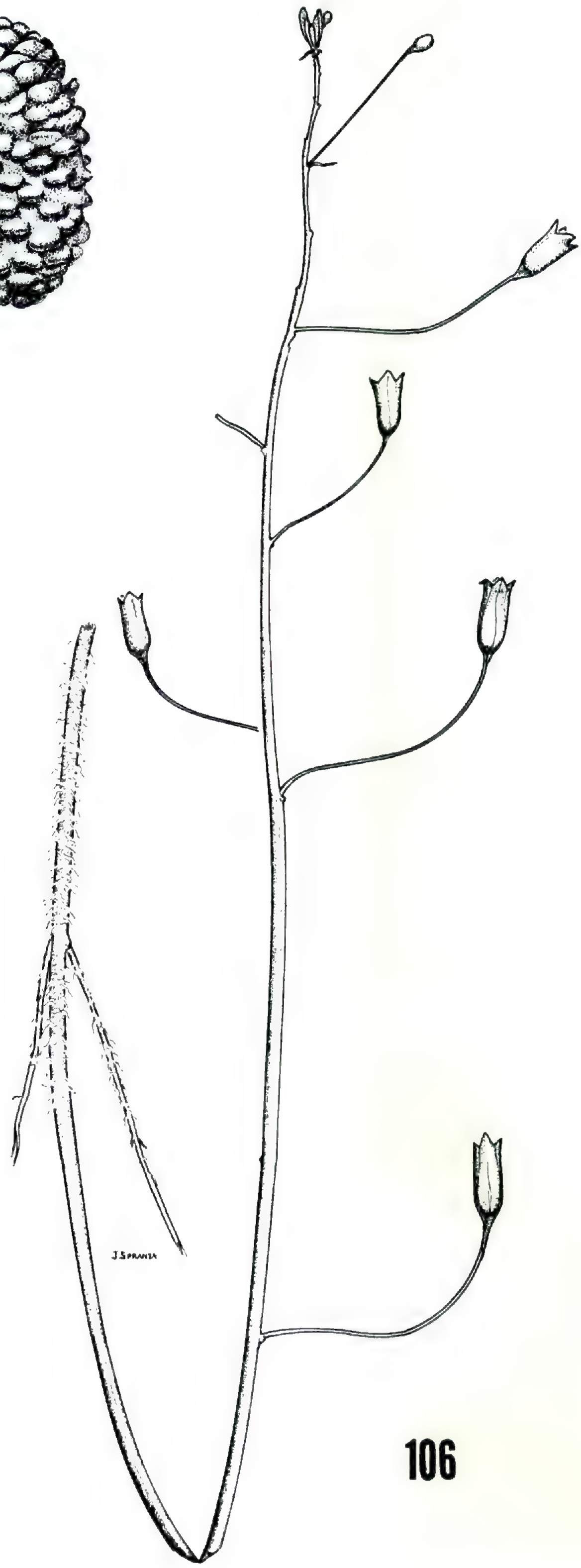

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narrowly obovate, long-clawed; the upper ones ca. 5 mm long, lanceolate, scarcely clawed, eglandular. *Fertile stamen* not known. *Staminode* ca. 5 mm long, angustate at base, obcordate at apex, white. *Style* ca. 2 mm long. *Capsule* ca. 8 mm long, ca. 3 mm thick, cylindrical-clavate, open at summit only. *Seeds* ca. 1 mm long, transversely tubercled and suberoded, black.

TYPE: Mexico, Sinaloa, Cuesta (or Cueva or Curva) del Diablo, Municipalidad Concordia, September 1919, *M. P. Dehesa 1561* (US).

Distribution (Fig. 34): Mexico, endemic in central Sinaloa, at lower elevations; apparently rare, and apparently known only from one gathering.

Specimen examined:
MEXICO. SINALOA: Concordia, Mazatlán, *Ortega 1561* (MEXU, number of type collection).

A rare species of which the type is the only known collection. Munz (1961) distinguished it from *Lopezia clavata* mainly by its larger flowers. In view of the wide variability of the latter, this distinction is unsatisfactory. More relevant dissimilarities are found in the pilosity of stems, morphology of upper petals, length of staminode, thickness of capsules, surface of seeds and to some extent also in leaf-margins and in the color of sepals and petals. The two species are very similar and further material of *L. sinaloensis* will be necessary before they can be compared adequately.

DOUBTFUL NAMES AND EXCLUDED SPECIES

Lopezia bracteata Rafin., Autikon Botanikon 13. 1840.—Description inadequate, authentic material unknown. Said to be from New Mexico; doubtfully *Lopezia*.

L. glazioui H. Leveille, Fedde Repert. Nov. Sp. 4: 226. 1907 = *Diplusodon virgatus* Pohl (Lythraceae).

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A NEW SPECIES OF *CISSUS* (VITACEAE) FOR CENTRAL AND SOUTH AMERICA

THOMAS B. CROAT[1]

ABSTRACT

Cissus pseudosicyoides is described as new. The species ranges from Costa Rica to Colombia. Though it has been confused in the herbarium with *C. sicyoides* L., it is probably more closely related to *C. biformifolia* Standley with which it shares dimorphic leaves and appressed T-shaped trichomes. It is most easily distinguished from *C. sicyoides* by having minute puberulence on most parts with occasional T-shaped trichomes and by having pubescent pedicels. It is distinguished from *C. biformifolia* by being densely puberulent and by having smaller greenish flower buds and smaller fruits.

Two unifoliate species of *Cissus*, *C. sicyoides* L. and *C. biformifolia* Standley, were reported in the *Flora of Panama* (Elias, 1968). In the course of my work on the Barro Colorado Island (Panama) flora, another species has been discovered.

Cissus pseudosicyoides, sp. nov.

Herba scandens cirrhosa; rami parvi et nervi foliorum trichomatibus brevibus inconspicuis, approximatisque necnon trichomatibus T-formibus, sparsis, adpressisque. Folia alterna, sicco nigrescentes; limbo foliorum majorum ovato-cordato, 9–15 cm longo, 9–12 cm lato, nervis lateralibus utroque latere 3–6; petiolis foliorum majorum 7–11 cm longis; limbo foliorum parviorum anguste ovatis, basi truncato aut obtuso aut acutato, 3–10 cm longo, 2–8 cm lato. Inflorescentia 1–4 cm longa; pedunculo florenti 2–10 mm longo, trichomatibus T-formibus densis adpressis; calyx expansus, ± crateriformis, 4-lobatus remote, alabastro latiorus; alabastrum ovoideum, 1.5–2 cm longum; petalum album aut cremeum (ruber aliquando). Fructus ± globosus, ad 6 mm diametro, viridis. Flores per initium tempus sicci.

Tendrilled herbaceous *vine*, probably ultimately arising from a woody stem; at least smaller stems, petioles, and veins of leaf blades (especially below) closely and inconspicuously puberulent; the same parts but also the axes of the inflorescence, pedicels, and leaf surfaces often sparsely pubescent with flattened, ± appressed T-shaped trichomes; stems of juvenile parts often white-speckled; *leaves* alternate, thin, usually drying dark, the larger ones borne below the inflorescence, ovate-cordate, as broad or nearly as broad as long, 9–15 cm long and 9–12 cm wide, with 3–6 pairs of lateral veins above sinus, with a single strong trunk vein extending into each basal lobe, the veins extending into apiculate teeth along the margin of the blade, the sinus about as deep as broad; *petioles* mostly 7–11 cm long; leaves higher on the stem and opposite the inflorescences usually narrowly ovate, smaller and with the base truncate to obtuse or acute at base (rarely cordate at base), mostly 3–10 cm long and 2–8 cm wide with petioles mostly 2–8 cm long, otherwise as the larger leaves. *Inflorescences* terminal or opposite upper leaves, small, congested, branched, umbelliform cymes 1–4 cm long, about as broad as long; peduncles mostly 2–10 mm long at anthesis (somewhat longer in fruit), densely appressed-pubescent with T-shaped trichomes, densely bracteate at apex, the bracts minute with margins glabrous or very in-

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ANN. MISSOURI BOT. GARD. 60: 564–567.

conspicuously ciliate; pedicels terete, 1.5–3.5 mm long, sparsely pubescent, the trichomes as on peduncles but usually smaller; *calyx* spreading, ± bowl-shaped, inconspicuously 4-lobed, narrower than the buds, nearly glabrous; *buds* ovoid, 1.5–2 mm long, drying with ridges along the margins of the petals; *corolla* of 4 free, broadly oblong petals, these obtuse and cucullate at apex inside, usually white or cream (rarely red); *stamens* opposite petals; filaments to ca. 1 mm long, equalling or longer than anthers; anthers nearly as broad as long, dehiscing laterally; *stigma* simple, to ca. 1.5 mm long. *Fruits* ± globose, to 6 mm in diameter, apparently green at maturity; pericarp and mesocarp thin; *seed* 1, round, only slightly smaller than the dimensions of the fruit.

HOLOTYPE: Panama. Canal Zone: Barro Colorado Island, "Clearing at laboratory; vine; fruits green; flowers greenish." 9 January 1969. *Croat 7017* (MO).

Flowers at the beginning of the dry season in December and January on Barro Colorado Island (rarely elsewhere as late as March) or in the rainy season (late July–October). Individual plants may flower for one month or more. The fruits develop promptly, usually are present with flowers, and are usually gone by March. They are probably dispersed by small- to mid-sized birds. It is not known whether the fruits become brightly colored or not. Observations on Barro Colorado Island indicate that the fruits are probably removed before turning color.

Cissus pseudosicyoides ranges from Guanacaste Province of Costa Rica to northern Colombia. It is widespread in lowland areas of Panama, principally from the Pacific slope in drier areas of tropical moist forest but is also known from premontane wet forest at Chiman and premontane dry forest at Juan Diaz in Panama Province.

COLOMBIA. MAGDALENA: Santa Marta, *Herbert H. Smith 1625* (MO, US, F). VAUPES: Río Guayabero, 240 m altitude, *Cuatrecasas 7576* (MO).

COSTA RICA. PUNTARENAS: Palmar Norte de Osa, *Allen 5450* (F, US). GUANACASTE: Vicinity of Tilaran, *Standley & Valerio 44935* (US); El Arenal, *Standley & Valerio 45062* (US). SAN JOSÉ: Basin of El General, altitude 675–900 m, *Skutch 4840* (F).

PANAMA. CANAL ZONE: Barro Colorado Island, North edge of laboratory clearing, *Croat 4274, 7017, 7396, 16550* (all MO); shore each side of Gross Point, *Foster 2048* (DUKE, MO); shore south of lab, *Wetmore & Abbe 38* (F, MO), *154* (F). Transisthmian highway about 19 miles from Colón, *Burch et al. 1001* (DUKE, F, GH, K, MO, NY, UC, US). DARIÉN: Vicinity of Santa Fé, Río Sabana, *Duke 4138* (GH, MO); Río Balsa between Manene and Tusijjuanda, *Duke 13575* (MO); Tucuti, *Terry & Terry 1400* (F, GH, MO). PANAMÁ: Boyd-Roosevelt Highway 1 mile N of Chagres River, *Blum & Tyson 1985* (MO); Chiman, *Lewis et al. 3336* (MO); San José Island, *Johnston 875* (GH, MO); Juan Diaz, *Standley 30553* (US); vicinity of Pacora, *Allen 1007* (MO, US). VERAGUAS: Puerto Mutis, *Tyson 6023* (MO, SCZ). LOS SANTOS: Tonosí, *Tyson et al. 2996* (MO).

Cissus pseudosicyoides Croat differs from the other unifoliate species of *Cissus*, *C. biformifolia* and *C. sicyoides*, in a number of ways. The differences among the three are outlined in Table 1.

Cissus pseudosicyoides bears superficial resemblance to some forms of *C. sicyoides*, principally because of its unifoliate leaves and small green flowers. *Cissus sicyoides*, a wide ranging species known from the southern United States, the West Indies, Mexico, Central America, and much of south America, is extremely variable in size and shape of leaves and degree of pubescence. The pubescence of the latter is uniformly villous. Generally leaves are ovate-oblong

TABLE 1. Comparison of unifolilate species of *Cissus* in Panama.

Cissus sicyoides L.	*Cissus pseduosicyoides* Croat	*Cissus biformifolia* Standley
Pubescence of smaller stems, petioles, and veins of lower leaf surface altogether lacking or of villous trichomes, these often crisped.	Pubescence of smaller stems, petioles, and veins of lower leaf surface of densely puberulent trichomes interspersed with fewer appressed T-shaped trichomes.	Pubescence of smaller stems, petioes, and veins of lower leaf surface altogether lacking or of whitish appressed T-shaped trichomes (rarely with a few sparse puberulent trichomes).
Leaves monomorphic; larger leaves at most rounded or truncate at base.	Leaves dimorphic; larger ones cordate at base.	Leaves dimorphic; larger ones cordate at base.
Midrib of blade markedly flattened, glabrous or villous.	Midrib of blade not at all flattened, minutely and densely puberulent.	Midrib of blade not at all flattened, usually glabrous.
Pedcels glabrous (Mexican collections sometimes pubescent but then with longer trichomes, never short or appressed).	Pedicels densely pubescent with both puberulent and dark T-shaped trichomes.	Pedicels with whitish T-shaped trichomes.
Calyx spreading, often prominently lobed, usually broader than the bud, much shorter than the corolla; buds mostly 1–1.5 mm long (dry), glabrous.	Calyx rather closely clasping base of bud, narrower than the bud, much shorter than the corolla; buds mostly 1.5–2 mm long (dry), glabrous.	Calyx spreading, often prominently lobed, broader than the bud and often enveloping to half of the base of the corolla; buds mostly 3–4 mm long (dry), often with sparse, whitish, T-shaped trichomes.
Fruits to 6 mm wide.	Fruits to 6 mm wide.	Fruits 8–10 mm wide.
Flowering not seasonal or at least not restricted principally to early dry season; usually flowering 2 or more times per year; plants with flowering and fruiting inflorescences on different parts of plant.	Flowering very seasonally, usually early dry season; plants ultimately bearing inflorescences in a succession of stages from bud through fruit.	Flowering mostly seasonally, most plants flowering in early dry season; plants ultimately bearing inflorescences in a succession of stages from bud through fruit.

and conspicuously pubescent but range to subrotund and nearly glaborus along seashores. Perhaps the easiest way to distinguish *C. sicyoides* from the other unifoliate species in Panama is by its glabrous pedicel. Both *C. pseudosicyoides* and *C. biformifolia* have varying amounts of pubescence on the pedicels. The trichomes are usually appressed and T-shaped.

Elias (1968) in the *Flora of Panama* treament of the Vitaceae included all known Panamanian specimens of *C. pseudosicyoides* with *C. sicyoides*. Despite its superficial resemblance to *C. sicyoides*, the new species is more closely related to *C. biformifolia* Standley. *C. biformifolia*, which ranges from Mexico to Venezuela, occurs only along the Caribbean coast of Panama in both tropical moist and tropical wet forest. It is distinguished by having large, red flowers (3–4 mm long in bud) and fruits 8–10 mm in diameter. Features shared in common between *C. biformifolia* and *C. pseudosicyoides* include dimorphic leaves, pubescence type and phenological behavior.

Although mature leaves of *C. biformifolia* are often nearly glabrous, the younger parts are usually conspicuously pubescent with whitish, appressed T-shaped trichomes. In addition, some parts, especially the veins of the lower leaf surface, are sometimes sparsely (rarely densely) puberulent. The larger stem leaves of both *C. biformifolia* and *C. pseudosicyoides* are ovate-cordate while the smaller leaves are acute to at most truncate at the base.

Cissus biformifolia and *C. pseudosicyoides* share similar phenological flowering and fruiting patterns, both flowering principally in the early dry season with a single prolonged flowering such that a single stem may bear all successive stages of development from flower buds at the apex to mature fruits farther down on the stem. In contrast, flowering is not seasonal in *C. sicyoides*. These plants flower two or more times per year for short intervals. A long succession of inflorescences are usually not produced on the same stem but when they are, fully mature fruits are not found on the same plant at time of flowering. Mature fruits may be found on the same plant at time of flowering, but they are usually quite removed from the flowering inflorescence and the result of an earlier flowering.

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The John S. Lehmann Building

In mid-1972 the herbarium and library of the Missouri Botanical Garden were moved to new quarters in the John S. Lehmann Building. The building is on two levels, with the entire herbarium storage facilities and offices occupying the lower level (20,850 square feet) and the library, herbarium workroom, and offices the upper (21,320 square feet). The building consists of cast-in-place concrete superstructure with double-thermopane, reflective glass walls.

The herbarium, about 2.5 million specimens, is stored in six compactor units. Such compactors have been used on smaller scales in several herbaria, *e.g.* Geneva, Perth, Utrecht, for some time. This storage system needs only half the amount of floor space occupied by standard herbarium cases of equal storage capacity.

From 1859 until 1891 the herbarium and library were housed in the Museum Building. This still stands and was modeled on plans of a building designed, but never built, for Kew. In 1891 the collections were moved to the Town House of Henry Shaw (who founded the Garden in 1859), which had been moved from downtown St. Louis to the Garden and rebuilt—brick-by-brick. A wing was added to the Town House in 1908, and the herbarium-library was stored there until the 1972 move.

The *Annual Report of the Missouri Botanical Garden* for 1909 stated that the Town House addition "promises to afford safe and convenient housing for the library and herbarium for a number of years." It did. The Lehmann Building has now assumed this role, on a much more convenient and modern scale.—*Editor.*

NOTES

A NEW *MATELEA* FROM PANAMA

Matelea as defined by Woodson (Ann. Missouri Bot. Gard. 28: 193–244. 1941) in his study of the North American Asclepiadaceae is the largest genus in the tribe Gonolobeae. Although ranging from the southern United States well into South America, the center of distribution of the genus appears to be the southern Mexico-Guatemala region with a possible secondary center in northern South America. There are, at present, eight species reported from Panama, although this number seems to increase with each new collecting trip. While most of the species occurring in Panama are found elsewhere in Central America, the more recently collected ones have definite South American affinities. The new taxon described here most resembles specimens in the herbarium at Missouri Botanical Garden which appear to represent two or three new taxa from South America. If indeed these are new, they will be described at a future date.

Matelea panamensis Spellman & Dwyer, sp. nov.—Fig. 1.

Folia elliptica integra, basi obtusa usque truncata, apice cuspidata. Inflorescentia extra-axillaris umbellata. Calyx extus hispidus intus glaber, lobis lanceolatis acutis. Corolla rotata, lobis late ovatis, apice brevi-cuspidatis, brunneis. Annulus faucis porcae angustae similis, ciliis albidis patulis ad 0.6 mm longis ornatus. Corona pallido-brunnea, lobis 5 altis annulo angusto conjunctis, eo columnam staminum adnato, lobis apice lato-reniformibus, ca. 1.5 mm latis et ca. 1.0 mm longis. Fructus anguste ovatus, 21 cm longus 9 cm latus, exocarpio in sicco lignoso crasso, endocarpio in sicco coriaceo crasso. Semina 1.5–1.7 cm longa et 0.8–1.1 cm lata, ala crassa lata proximale erosa, ca. 3.0–3.5 mm lata, coma 2–3 cm longa.

Vine, suffruticose, the stems hollow. Stems, petioles, and main veins of the leaves pubescent, the hairs of two types, short bulbous ones mostly less than 0.2 mm long overtopped by multicellular brown ones 3–5 mm long. *Leaves* elliptic, entire, obtuse to truncate at the base, cuspidate at the apex; margins ciliate, the hairs long and multicellular, the blades discolor, the upper surface with scattered multicellular hairs, the lower scabrous intercostally; petioles 5.5–6.0 cm long; lamina 12–15 cm long and 7.5–9.0 cm wide. *Inflorescence* extra-axillary, umbellate, pubescent as on the stems, several flowered; peduncle ca. 2.0 cm long; pedicels ca. 1.5 cm long. *Calyx* densely brown pubescent abaxially, glabrous adaxially, ca. 1.4 cm in diameter, the 5 lobes lanceolate, acute, 5–6 mm long and 2–2.5 mm wide, a single conical gland in each sinus. *Corolla* rotate, ca. 2.2 cm in diameter, the 5 lobes, broadly ovate and shortly cuspidate at the apex, ca. 8 mm long and 8 mm wide, purplish-brown, hairs on the adaxial surface short, inconspicuous, appressed, gray, most abundant on the basal half of the lobes, the abaxial pubescence of the same type as on the stems, the multi-cellular ones prominently disposed in a thin band at the base of the lobes. *Faucal annulus* a low thin ridge, ca. 0.1 mm high or less, with dense, white, spreading hairs to 0.6 mm long. *Corona* carnose, 5 lobed, the lobes connected by a narrow annulus which is accrescent to the staminal column, each broadly reniform lobe joined to the annulus by a thin stalk which is ca. 1.1 mm long by ca. 0.4 mm wide, the lobes themselves ca. 1.0 mm long and ca. 1.5 mm wide, their margins slightly crenate. *Gynostegium* ca. 2.0 mm high, the head ± pentagonal, ca. 2.5 mm in

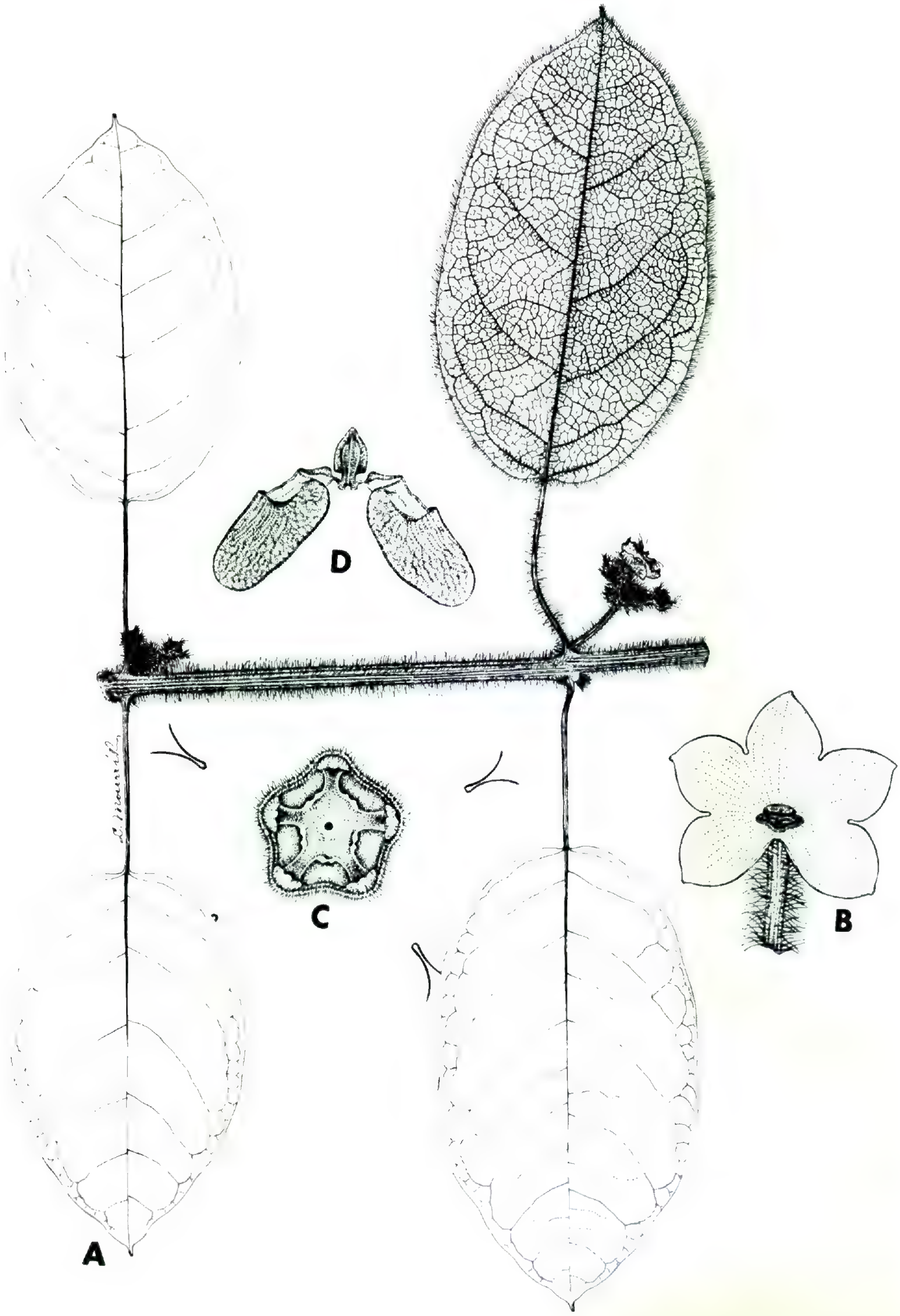

FIGURE 1. *Matelea panamensis* Spellman & Dwyer.—A. Flowering stem (× 0.4).—B. Flower (× 1.1).—C. Faucal annulus and corona (× 2.5).—D. Pollinia (× 20). [After *Dwyer 8300* (MO, holotype).]

diameter, depressed in the center, covered by a thick membrane which becomes white in drying. *Pollinia* inserted horizontally, flattened truncate-elliptic, ca. 0.9 mm long exclusive of the translator, 0.4 mm wide. *Translators* ca. 0.3 mm long and half as wide. *Corpusculum* ca. 0.3 mm long and 0.2 mm wide. *Fruit* ovate, 21 cm long and 9 cm wide, with a broad, low dorsal ridge, the fruiting pedicel attached about 5 cm from the end, exocarp thick and woody when dry, the endocarp thick and leathery. *Seeds* 1.5–1.7 cm long and 0.8–1.1 cm wide, the wing thick and ca. 3.0–3.5 mm wide, erose proximally, the silky coma 2–3 cm long.

Holotype: PANAMA. COCLÉ PROVINCE: Cerro *Pilón*. 2500–3000 feet elevation, *Dwyer 8300*. (MO).

A quite distinctive species, *Matelea panamensis* has no close relatives among other taxa of Central America or Panama. It is readily distinguished by the long, dense, brown pubescence on the vegetative parts and calyx and by the dark brown rotate corolla.—*David L. Spellman* and *John D. Dwyer, St. Louis University* and *Missouri Botanical Garden.*

TRIBULUS CISTOIDES IN PANAMA

In my treatment of the family Zygophyllaceae for the *Flora of Panama* (Ann. Missouri Bot. Gard. 56: 177. 1969), the possibility of *Tribulus cistoides* L. occurring on the Isthmus was indicated. *Tribulus terrestris* L., a warm-temperate zone plant known only rarely from the tropics, had been collected once in the Canal Zone (Frijoles, railroad tracts, 20 May 1918, *Killip 3445* in part (US)), while *T. cistoides*, native to tropical Africa, apparently had not. On a recent trip to the Herbarium of the New York Botanical Garden, however, I discovered a collection of *T. cistoides* from the Canal Zone (Between Mt. Hope and Santa Rita Trail, 25 Feb 1905, *Cowell 90* (NY)). Both species are plants of dry disturbed habitats, and both Isthmian collections undoubtedly represent waifs that have failed to form persistent populations.—*Duncan M. Porter, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560.*

SEVEN NEW COMBINATIONS IN *BAUHINIA*

In the course of preparing a revision of the New World species of *Bauhinia*, it was ascertained that seven new combinations were needed to better align certain taxa. It is deemed better to publish these new combinations as a note at this time rather than wait until the revision is completed in approximately two years. Thus, the following new combinations in *Bauhinia* are proposed.

Bauhinia aculeata subsp. **grandiflora** (Juss.) Wunderlin, *stat. nov.* Basionym: *Bauhinia grandiflora* Juss. *in* Poir., Encyc. Suppl. 1: 600. 1811.

Bauhinia beguinotii var. **gorgonae** (Killip *ex* Cowan) Wunderlin, *stat. nov.* Basionym: *Bauhinia gorgonae* Killip *ex* Cowan, Bol. Soc. Venez. Ci. Nat. 22: 281. 1961.

Bauhinia forficata var. **platypetala** (Burch. *ex* Benth.) Wunderlin, *stat. nov.* Basionym: *Bauhinia platypetala* Burch. *ex* Benth. *in* Mart., Fl. Bras. 15(2): 198. 1870.

Bauhinia guianensis var. **kunthiana** (Vog.) Wunderlin, *stat. nov.* Basionym: *Bauhinia kunthiana* Vog., Linnaea 13: 312. 1839.

Bauhinia hymenaeifolia var. **stuebeliana** (Harms) Wunderlin, *stat. nov.* Basionym: *Bauhinia stuebeliana* Harms, Fedde Repert. Sp. Nov. 19: 65. 1923.

Bauhinia longicuspis var. **paraensis** (Ducke) Wunderlin, *comb. nov.* Basionym: *Bauhinia holophylla* var. *paraensis* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 52. 1925.

Bauhinia stenoloba (Britt. & Killip) Wunderlin, *comb. nov.* Basionym: *Schnella stenoloba* Britt. & Killip, Ann. New York Acad. Sci. 35: 163. 1936.

—*R. P. Wunderlin, Missouri Botanical Garden.* Present address: *Department of Botany, University of South Florida, Tampa, Florida 33620.*

A NEW SPECIES OF PROTEACEAE FROM PANAMA

Roupala percoriacea A. Gentry, sp. nov.

Arbor parva. *Folia* simplicia, ovata vel elliptico-ovata, percoriacea, glabra, integra margine revoluto. *Racemi* axillares strigosi. *Tepala* 6–7 mm longa, supra insertiones staminum reflexa. *Stamina* in tepalis inserta, antheris peranguste oblongis. *Glandes* hypogynae quatuor. *Pistillum* 6–7 mm longum, ovario breviter strigoso. *Fructus* folliculus compressus glaber apice apiculato recurvato basi stipitata.

Small *tree*, 4–5 meters tall, ca. 3 cm in diameter; branchlets terete, glabrous. *Leaves* simple, ovate or elliptic-ovate, 5.5–16 cm long and 3–10 cm wide, obtuse to acute or abruptly short acuminate at apex, more or less rounded at base, percoriaceous, glabrous, the margin perfectly entire, conspicuously revolute; petiole 1–3 cm long, usually inconspicuously puberulent above. *Inflorescence* an axillary raceme, rachis 6–11 cm long, strigose-puberulous with reddish trichomes; flowers borne in pairs. *Tepals* linear-oblanceolate, 6–7 mm long, less than 1 mm broad, the upper 2 mm (above stamen insertion) reflexed, somewhat strigose without, glabrous within. *Stamens* inserted about 4 mm from bases of tepals; anthers linear oblong, 1.5–2 mm long and 0.5 mm wide; filaments less than 0.5 mm long. Hypogynous *glands* 4, less than 0.5 mm long, glabrous. *Pistil* 6–7 mm long; ovary 1 mm long, less than 1 mm wide, very shortly strigose; style 5–6 mm long, glabrous; pedicels 1–2 mm long; strigose-puberulent with reddish trichomes. *Fruit* a compressed follicle, 3–3.3 cm long and 1.5–1.6 cm wide, the tip contracted into a recurved apiculation 2–3 mm long, the base contracted into a stipe 4–5 mm long, glabrous; seeds not seen.

Holotype: PANAMA. PANAMÁ: Cerro Jefe, 10.1 miles from Tocumen circle, altitude 800–1000 meters; small tree, 1 inch diameter, 4 meters tall, flowers white, few old fruits persistent, leaves coriaceous, *A. Gentry* 2887 (MO; isotypes to be distributed).

Known only from the premontane rain forest life zone near the top of Cerro Jefe. In flower in December.

PANAMA: PANAMÁ: Cerro Jefe, ca 2800 feet, tree 15 feet tall, fruit green, *Dwyer et al. 7246* (MO).

This species is remarkable in the genus on account of its exceedingly coriaceous leaves, being matched in this respect only by *R. chimatensis* Steyermark and *R. sororopana* Steyermark of the 30 species examined by the author. In Sleumer's key (Bot. Jahrb. Syst. 76: 142–153. 1954.) it is related by its glabrous, entire leaves, pubescent ovary and rachis, and tepals 6–7 mm long to *R. thomesiana* Moricand of Bahia, Brazil, which is totally different in much smaller, attenuate, suborbicular leaves and glabrous perianth. *Roupala chimatensis* from the Guiana highlands of Bolivar, Venezuela, is perhaps its closest relative but differs in its furfuraceous indumentum, longer inflorescence with a thick rachis, and longer perianth. The recently described *R. schultzii* A. Mennega from Surinam was related by its author to *R. chimatensis* but differs from both that species and *R. percoriacea* in its trinerved leaves.

The leaves of the type specimen of *Roupala percoriacea* are conspicuously dark red but this probably reflects its having been subjected to the intense heat of a fire at Summit Herbarium, Panama, and should not be regarded as a valid taxonomic character.

The only other Panamanian species of *Roupala* is the variable *R. montana* Aubl., which occurs in the same area as *R. percoriacea*, having been collected on the lower slopes of Cerro Jefe. The following key separates the two Panamanian species.

1. Leaves percoriaceous, margins entire and revolute, petioles thick; tepals 7 mm or less long, reflexed only above stamen insertion; anthers less than 2 mm long; ovary very short-strigose, sometimes appearing almost lepidote; fruit apex recurved ..... *Roupala percoriacea*
1. Leaves chartaceous to subcoriaceous, the margins usually coarsely serrate or somewhat undulate, not revolute, the petioles slender; tepals 7 or more mm long, reflexed from base; anthers more than 2 mm long; ovary densely strigose, conspicuously puberulent; fruit apex straight ..... *Roupala montana*

—*A. Gentry, Missouri Botanical Garden.*

THE 1973 GREENMAN AWARD

The sixth Jesse M. Greenman Award was won by William R. Anderson, The New York Botanical Garden, for his paper "A monograph of the genus *Crusea* (Rubiaceae)" (Mem. New York Bot. Gard. 22(4): 1–28. 1972).

The Greenman Award is a cash prize of $250, awarded yearly by the Alumni Association of the Missouri Botanical Garden, in recognition of the paper judged best in plant systematics published during the *previous* year. To qualify for the award a paper must be based on a doctoral dissertation. Papers published in *1973* will be considered for for next year's award until 1 May 1974. Reprints of such papers should be sent to Peter H. Raven, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.—*Editor.*

The previous two issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 59, No. 3, pp. 323–478, and Vol. 60, No. 1, pp. 1–167, were published on 15 May 1973 and 22 September 1973, respectively.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum*.

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

All illustrative material should be mounted on stiff cardboard. If the originals are too large to be conveniently mailed, photographic reductions should be submitted. The maximum size of a printed illustration is 5 × 7¾ in., and therefore, the height of an illustration must not exceed about 1.5 its width. Figures are numbered consecutively, since they are not printed as "plates." Numbering must be done with a mechanical device or with dry-transfer lettering and never by hand. The amount of reduction should be noted on the back of each illustration, together with the figure numbers, author's name and title of the paper. Photographs should be sharp, glossy prints. Numbering should be applied directly to the surface of the photograph. Several photographs may be assembled to form a composite block, and each photograph should be numbered separately. The individual photographs should be mounted with the interior edges flush. Line drawings are prepared with India ink and must never be placed in the same block with photographs. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

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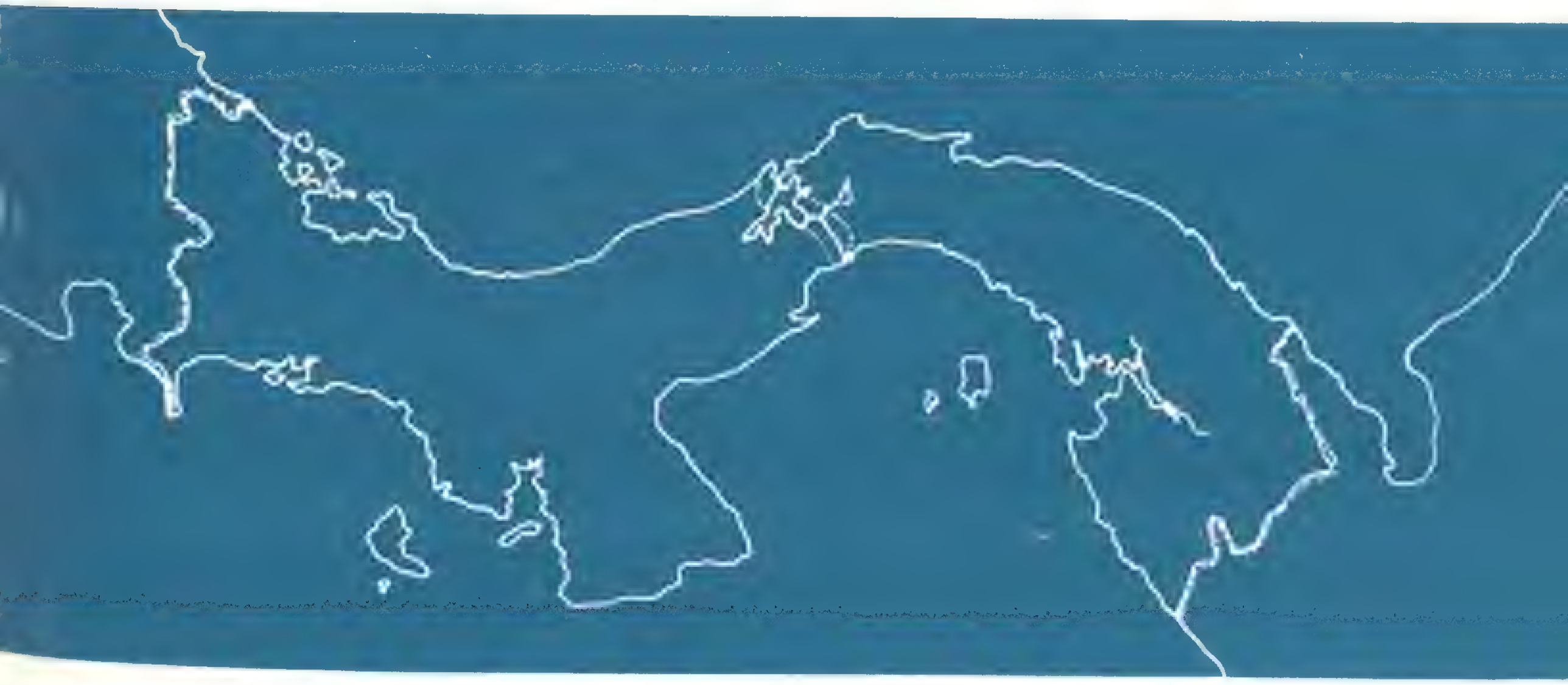
The *Flora of Panama* treats the various families of indigenous and naturalized plants of the Republic of Panama and the Panama Canal Zone. Each family is dealt with in a critical manner with synonymy, descriptions, discussions, illustrations, and citation of representative Panamanian collections for each species. The *Flora* appears in the ANNALS OF THE MISSOURI BOTANICAL GARDEN as contributions accumulate, but all parts are available separately through Allen Press, Inc., 1041 New Hampshire, Lawrence, Kansas 66044.

VOLUME 60
1973
NUMBER 3

ANNALS OF THE
Missouri Botanical Garden



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ANNALS OF THE
Missouri Botanical Garden

The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden. Papers originating outside the Garden will also be accepted. The ANNALS appears three times a year, and three numbers, totaling about 400 pages, constitute a volume.

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Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.
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ALLEN PRESS, INC. PRINTED IN U.S.A. LAWRENCE, KANSAS

VOLUME 60
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NUMBER 3

ANNALS OF THE
Missouri Botanical Garden

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 170. SOLANACEAE[2]

W. G. D'ARCY[3]

Herbs, *shrubs*, *trees*, *lianas* or *epiphytes*, often armed; stems with bicollateral bundles, latex absent, alkaloids often present. Leaves alternate or paired, estipulate, simple or pinnately compound, entire or variously lobed, glabrous or pubescent with simple, dendritic, stellate, scutellate, and often glandular hairs,[4] sometimes armed, degenerate stomata present, sometimes with single guard cells. *Inflorescence* terminal or axillary, often becoming lateral, a panicle, raceme, fascicle or sometimes a solitary flower, bracts or bracteoles sometimes present. *Flowers* complete, mostly perfect but the first flowers sometimes staminate, rarely dioecious, from small to very large, sometimes fragrant, (4–)5(–9)-merous, actinomorphic or zygomorphic; the calyx gamosepalous, prefloration valvate or complete, the apex lobed or truncate, splitting or stretching to permit egress of

[1] Assisted by National Science Foundation Grant GB-5674 (Thomas B. Croat, principal investigator).

[2] Revised portion of a Ph.D. thesis submitted to Washington University under the direction of Prof. Walter H. Lewis.

[3] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

[4] Stellate hairs (stellae) may be sessile or stalked, the stalks being multiseriate and terminated by branches or arms (radii) which come off at one point in one plane (porrect) or at many angles (multangulate). Beyond the point of radii insertion the axis is continued by a midpoint which may bear a terminal gland. The radii may be few (pauciradiate) or very numerous (echinoid). Stellae which develop stout woody stalks are bristles, and the radii are usually visible at the apex at some stage of development. Still stouter stalks are referred to as thorns or spines and may be needle-like (acicular) or hook-like (recurved). Seithe (1962) has elucidated developmental sequences of these trichome types. Stellate pubescence is referred to as sparse, dispersed or dense, dense pubescence being when the radii of neighboring stellae overlap, dispersed when there is a general covering of stellae but the midpoints do not overlap and sparsely pubescent indicates scattered stellae widely separated from one another.

ANN. MISSOURI BOT. GARD. 60: 573–780. 1973.

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flower or fruit, sometimes circumscissile, sometimes with an epicalyx of a series of secondary teeth or umbos or a basal swelling, often accrescent in fruit; corolla sympetalous, prefloration valvate, induplicate valvate, imbricate or quincuncial, rarely incomplete, tubular, tubiform, campanulate or rotate; the stamens borne on the corolla tube, mostly 5 or reduced to 4, 2, or 1 and staminodes sometimes present, filaments sometimes appendaged, the anthers mostly 2-loculed for part or all of their length, the thecae parallel and connected, the anthers longitudinally dehiscent or opening by terminal pores; the ovary superior (partly inferior in *Solandra*), of 2 united carpels, and the locule number sometimes increased or reduced by proliferation or reduction of the septum, a hypogenous or rarely perigynous disc sometimes present; ovules mostly many in each locule, tenuinucellate, anatropous or slightly amphitropous, the placentae elaborated, mostly axile; the style terminal on the ovary, slender, simple, the stigma small or relatively large and elaborated. *Fruit* mostly a berry or capsule; the seeds often compressed, rarely winged or pubescent, the embryo straight or curved and peripheral, terete or flattened, not plicate; the endosperm fleshy.

The Solanaceae includes some 80 genera of diverse form. The family is strongly centered in America south of the United States with many species of a few genera in Africa. Species are found in most parts of the world and several isolated genera occur in Australia. Seven of the genera include more than fifty species. Only four genera—*Lycium* (80–90 species), *Physalis* (100), *Solanum* (over 1,400), and *Datura* (15)—occur both in America and across the Old World, but several genera are common to America and the Far East, and *Schwenkia* occurs in both America and Africa. Only about a dozen monotypic genera and only nine genera with two or three species are generally recognized today. Some 14 endemic genera occur in temperate South America. The type is *Solanum* L.

The family includes important food (potato, capsicum, tomato, lulo, pepino, ground cherry), drug (belladonna, atropine, tobacco, vodka, mandrake), and ornamental (petunia, tree potato, galan de noche, browallia, nicotiana, lycium, cestrum, orchid-flower) species as well as a host of noxious weeds (nightshades, bittersweet, arana gato, etc.). Although some species grow to large size, none are known for their wood.

Useful references:

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a. Anthers dehiscing by terminal pores (sometimes longitudinally as well).
  b. Anther connectives strongly thickened and evident the whole length of the anther; inflorescence arising at a dichotomy of the stem; fruit pendant on an elongate axis; calyx lobes present and in flower not splitting at the sutures ..... 6. *Cyphomandra*
  bb. Anther connectives not thickened, not evident the whole length of the anther (dorsal surface of anthers may be darkened); inflorescence variously situated; fruit erect or pendant; calyx lobes present or absent, often splitting at the sutures, lateral teeth sometimes present.
    c. Calyx with 10 vascular ribs, the apex truncate, stretching to permit egress of corolla and fruit, up to 10 teeth often arising from the side of the calyx; peduncles mostly wanting; leaves simple, entire ..... 11. *Lycianthes*
    cc. Calyx with 5 vascular ribs, mostly splitting at the sutures to permit egress of corolla and fruit; (4–)5(–6) apical teeth mostly present; peduncles mostly present; leaves often compound, lobed or toothed ..... 20. *Solanum*
aa. Anthers dehiscing longitudinally without apical pores.
  d. Stamens 4 or fewer; flowers mostly narrowly tubular or salverform; plants terrestrial.
    e. Fruit a dry capsule; seeds less than 0.8 mm across; weak or sprawling herbs mostly less than 50 cm tall.
      f. Corolla tubular, the lobes minute; calyx less than 3 mm across ..... 18. *Schwenckia*
      ff. Corolla salverform, the lobes conspicuous; calyx more than 4 mm across ..... 1. *Browallia*
    ee. Fruit a berry, juicy, custardy, fleshy or hard and leathery; seeds more than 1 mm across; tree, shrub or erect herb (sometimes flowering turoin) mostly more than 50 cm tall.
      g. Fruit custardy and leathery or fleshy, more than 15 mm across; seeds prismatic; flowers more than 20 mm long; anthers rounded or emarginate; tree or shrub ..... 3. *Brunfelsia*
      gg. Fruit a juicy, shiny berry, less than 12 mm across; seeds compressed discoid; flowers less than 20 mm long; anthers pointed, often apiculate; herb or subshrub rarely tree ..... 21. *Witheringia*
  dd. Stamens 5 or more; flowers of various shapes; plants terrestrial or hemi-epiphitic.
    h. Flowers more than 8 cm long.
      i. Terrestrial herbs or shrubs; flowers not yellow; leaves membranaceous; corolla lobes with elongate tips.
        j. Ovary and fruit elongate, 2-loculed; flowers pendulous; calyx markescent ..... 2. *Brugmansia*
        jj. Ovary and fruit rotund, 4-loculed, flowers held erect or at an angle to the ground; calyx circumscissile ..... 7. *Datura*
      ii. Vines or epiphytic shrubs; flowers yellow; leaves coriaceous; corolla lobes crenate to fimbriate without elongate tips ..... 19. *Solandra*
    hh. Flowers less than 8 cm long.
      k. Corolla tube less than 9 mm long, corolla mostly rotate or broadly campanulate.
        l. Calyx accrescent and enveloping the fruit.
          m. Corolla rotate, the margin unlobed; fruiting calyx mostly invaginated at the base ..... 16. *Physalis*
          mm. Corolla rotate or campanulate with manifest lobes; fruiting calyx not invaginated at the base.
            n. Fruiting calyx completely enveloping the fruit, the berry not tightly filling the calyx; anthers rounded; herb ..... 8. *Deprea*
            nn. Calyx tight against the berry wall, the berry emerging at the apex; anthers pointed; herb or sub-shrub ..... 21. *Witheringia*
        ll. Calyx not enveloping the fruit, if accrescent then the lobes flaring wide or recurved.
          o. Anthers tightly coherent by lateral grooves and ventral pubescence; seeds pubescent; leaves mostly compound ..... 12. *Lycopersicon*
          oo. Anthers free (sometimes connivent); seeds glabrous; leaves simple; mostly entire.
            p. Calyx conspicuously accrescent, in fruit the lobes deltoid, wide-flaring; corolla rotate; berry black ..... 9. *Jaltomata*

pp. Corolla hardly accrescent, in fruit the lobes neither deltoid nor wide-flaring; the berry not black.
q. Calyx deeply lobed, fruit not exceeding the calyx lobes; hemi-epiphytic shrubs ..... 13. *Markea*
qq. Calyx not deeply lobed, fruit greatly exceeding the calyx; terrestrial herbs, rarely high climbing.
r. Flowers white or nearly so; fruit a dry or fleshy berry; anthers rounded, not apiculate ..... 4. *Capsicum*
rr. Flowers yellowish, brownish, purplish, etc., rarely white; fruit a juicy berry; anthers pointed, often apiculate ..... 21. *Witheringia*

kk. Corolla tube more than 10 mm long, corolla mostly tubular, tubiform, or narrowly campanulate, not rotate or broadly campanulate.
s. Viscid pubescent herbs; seeds minute; cultivated plants.
t. Plants erect, more than 60 cm tall; flowers arising from a solitary leaf (bract); calyx lobed about halfway down; fruits more than 15 mm long ..... 14. *Nicotiana*
tt. Plants sprawling, less than 60 cm tall; flowers arising from a pair of leaves (bracts); calyx lobed to near the base; fruits less than 12 mm long ..... 15. *Petunia*
ss. Plants not viscid pubescent; herbs, shrubs, trees or vines; seeds 0.5 mm or more across; cultivated or wild plants.
u. Fruit not exceeding the calyx lobes; hemi-epiphytes.
v. Inflorescence a congested, spherical panicle; apical, ovuliferous portion of ovary contracted into a stylar base; corolla narrowly tubular, only slightly (4–8 mm) exserted from the calyx and pubescent with simple hairs ..... 17. *Rahowardiana*
vv. Inflorescence more or less open, not spherical; ovary not apically contracted into a stylar base; corolla tubular or campanulate, if tubular then long-exserted from the calyx and pubescent with stellate hairs.
w. Corolla narrowly tubular, conspicuously stellate pubescent outside, corolla lobes imbricate ..... 10. *Juanulloa*
ww. Corolla campanulate or broadly tubular, puberulent with simple hairs or glabrous outside; corolla lobes valvate ..... 13. *Markea*
uu. Fruit greatly exceeding the calyx (calyx sometimes deciduous); terrestrial shrubs or herbs.
x. Calyx deciduous, fruit with spines or tubercules, more than 12 mm across; leaves mostly lobed or sinuate margined; corolla tubiform, flaring at the apex ..... 7. *Datura*
xx. Calyx persistent; fruit smooth, less than 12 mm across; leaves entire; corolla narrowly tubular, sometimes expanded but not flaring at the apex ..... 5. *Cestrum*

1. BROWALLIA

Browallia L., Sp. Pl. 631. 1753; Gen. Pl., ed. 5. 278. 1754. TYPE: *Browallia americana* L.

Brouvalea Adans., Fam. 2: 211. 1763.

Branched, unarmed *herbs* to 70 cm tall; stems terete, glabrous or pubescent, the hairs simple, sometimes glandular and viscid. *Leaves* ovate, to 6 cm long, the margins mostly entire; petioles slender, slightly winged, sometimes reduced; minor leaves present or not. *Flowers* solitary, axillary, the subtending leaves sometimes reduced, the pedicels short but becoming longer in fruit, deciduous at the base; calyx tubular-campanulate with simple or glandular hairs, drying with prominent longitudinal veins, lobed less than ⅓ the way down, the lobes 4 or 5,

deltoid to lanceolate, sometimes rounded, becoming larger in fruit, exceeding but not enveloping the capsule, the tube sometimes inflated, strongly angled; corolla salverform, zygomorphic with a bulbous enlargement at the top of the greenish tube, the limb large or small, the mouth very small; stamens 4, sometimes with a staminode or rarely a fifth fertile anther, didynamous, inserted just above and below the expansion in the corolla tube, the upper pair with flattened, curved, pilose filaments which close the mouth of the tube, their anthers each with one obsolete theca, the lower pair with basally geniculate filaments and smaller, 2-thecate anthers; the disc obsolete; ovary subsessile, glabrous or pubescent, 2-loculed, the ovules many on a large placenta, stigma elaborately expanded into a furrowed wafer compressed between the anthers, stigmatic on the distal rim. *Fruit* an erect 2-valved, coriaceous or chartaceous, many seeded, septicidally short-dehiscent capsule; seeds minute, prismatic, foveate; embryo straight or slightly curved, cotyledons ovate on a broad radicle. Chromosomes $n = 22$, 44 (24).

Browallia is closely related to a number of species now considered to belong to other genera, *e.g. Leptoglossis*, *Brunfelsia*, *Schwenckia* and *Salpiglossis* (sensu lato), and further study of these groups may discover species which belong in *Browallia*. In all of these genera except *Salpiglossis* (sensu stricto), the mouth of corolla is sealed by various alterations of anther, filament, or stigma. In *Browallia*, the mouth is sealed by two flattened, pilose filaments which arch over the anthers and stigma, and in age, the stigma may force its way past the filaments. In the related species examined, the filaments, although they may be somewhat curved and flattened, do not take effective part in sealing of the corolla mouth. Upon study of the full range of mechanisms for corolla closure, it may be decided that members now in other genera which have expanded stigmas, reduced anthers and thecae, and also curved filaments, but which close the corolla mouth with the side of an anther, the base of the stigma or other part, are really best considered congeneric with *Browallia*. *Browallia* is further distinct from *Brunfelsia* in its herbaceous rather than woody habit.

Browallia is a small genus native to Central America and tropical South America which has been widely dispersed through the influence of post-Colombian man. The two species treated here are widely grown for ornament in other parts of the world. One of them is naturalized in the Antilles. Both species are known in both colored and white forms, and while they are usually easily distinguishable by their flower size, the two species are also quite distinct in other characters. The considerable differences between the two species argues for placing them in separate, although monotypic, sections of the genus.

In all, twenty-six species have been described in the genus, but study of the illustrations and type material upon which they are based suggests that most should be reduced to but two species of *Browallia*,[5] the remainder belonging to

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[5] In addition to names indicated for the two Panamanian species and the synonyms listed under them, the following names have appeared in the genus *Browallia*.

Browallia alienata L., Syst. Nat., ed. 10. 1118, based on Mill., Fig. Gard. Dict. [Ic.] No. 68. 1760. = *Ruellia paniculata* [Acanthaceae] fide *Index kewensis*.

genera in other families. In spite of the redundancy of names for the two species native to Panama, there are specimens in a number of herbaria which may be "good," undescribed species of *Browallia.*

The genus takes its name from John Browal, 1707–55, magistrate and botanical writer of Upsalla, later Bishop of Abo (Finland), friend of Linnaeus.

a. Corolla large, the tube mostly over 3 cm, the limb mostly over 5 cm across, the lobes pointed, the eye not sharply defined; calyx tube inflated; ovary glabrous on top; staminode or fifth stamen sometimes present; tetraploid species; rare in the wild in Panama (B. sect. *Leiogyne*) ..... 2. *B. speciosa*

aa. Corolla small, the tube mostly less than 3 cm, the limb mostly less than 2 cm across, the lobes rounded or emarginate, the eye sharply defined; calyx tube not inflated; ovary pubescent on top; staminode and fifth stamen wanting; diploid species; common in the wild in Panama (A. sect. *Browallia*) ..... 1. *B. americana*

A. Section **Browallia**

Sect. *Eubrowallia* Miers, Ann. Mag. Nat. Hist., ser. 2. 5: 207. 1850. LECTOTYPE: *B. demissa* L. (= *B. americana* L.).

1. **Browallia americana** L., Sp. Pl. 631. 1753. TYPE: Hort. Cliff., (BM, not seen, the original seed source was Panama [Miller, 1768, '*Browallia*']).

B. demissa L., Syst. Nat., ed. 10. 1118. 1759; Sp. Pl., ed. 2. 879. 1763. TYPE: Based on same specimen as *B. americana* L.
?*B. elata* L., Syst. Nat., ed. 10. 1118. 1759, *fide* Index Kewensis.
B. viscosa H.B.K., Nov. Gen. Sp. 2: 373. 1818: TYPE: Colombia, *Bonpland* (P).
B. linnaeana Spreng., Syst. 2: 808. 1825. TYPE: Based on *B. elata* and *B. demissa* L.
B. grandiflora Graham, Edin. Phil. Jour. 1830. TYPE: Seeds from Peru, *Cruckshanks s.n.* (K).
B. cordata D. Don., Gen. Syst. 4: 478. 1837. TYPE: Based on *B. grandiflora* Lindl., non Graham, seeds from Peru, collector not indicated (K). This material may or may not be authentic. Identity of the taxon is clear from the Lindley plate.
B. lactea G. Don *in* Sweet, Hort. Britt. 506. 1839, nomen nudum.
B. peduncularis Benth. *in* DC., Prodr. 10: 197. 1846. SYNTYPE: *Barklay s.n.* (BM).
B. tenella Miers, Ann. Mag. Nat. Hist., ser. 2. 5: 205. 1850. TYPE: Argentina, *Miers s.n.* (BM).
B. nervosa Miers, Ann. Mag. Nat. Hist., ser. 2. 5: TYPE: Ecuador, *Barklay 740* (BM).
B. dombeyana Damm., Bot. Jahrb. Syst. 37: 642. 1906. TYPE: Peru, *Dombey 61* (BM).
B. melanotricha T. S. Brandeg., Univ. California Publ. Bot. 6: 61. 1914. TYPE: *Purpus 6662* (BM, GH, MO).

Erect or straggling *herb* to 70 cm tall; stems mostly green, puberulent with short, mostly forward directed, simple or glandular hairs. *Leaves* ovate, to 5 cm long, acute or acuminate apically, truncate, obtuse or short acuminate basally, margins entire or nearly so, above glabrous or with scattered simple hairs on the lamina, beneath puberulent on the major veins; petiole half as long as the leaf or less. *Pedicels* erect, 3–5 mm long, puberulent, with very fine forward directed, sometimes glandular hairs. *Flowers* showy, the calyx 5–10 mm long, glabrate or

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Browallia capitata β angustifolia Benth., Gray Herb. Card Index, err. *Brunfelsia capitata.*
Browallia humifusa Forsk., Fl. Aegypt. Arab. 112. 1775. = *Striga humifusa* Benth., [Scrophulariaceae] fide *Index kewensis.*
Browallia jamesonii Benth. *in* DC., Prodr. 10: 197. 1846. = *Streptosolen jamesonii* (Benth.) Miers.
Browallia texana Torr., Bot. Mex. Bound. 156. 1859. = *Leptoglossis viscosa* (Torr.) Gray.
Browallia fruticosa Larrañaga, Escrit. D. A. Larrañaga, Atlas 1, *tab.* 67. 1927, nomen nudum.
Browallia lactea Hort. *ex.* Spreng., *in* L., Syst. Veg., ed. 16. 2: 308. 1825, nomen nudum.

with scattered larger, simple, often glandular hairs on the outside, lobed about ¼ the way down, the lobes pointed or rounded, the tube strongly angled becoming broadly cupular in fruit; corolla blue, mauve, purple or white, salverform, the tube 12–15 mm long, puberulent, the limb 10–14 mm across, puberulent on the ribs beneath; stamens 4, filaments of the upper pair flattened and broadened into a curved, strap-like structure, densely pilose with dendrictic, colored hairs, the lower pair only slightly flattened and sparsely pilose, the anthers yellow; ovary 1–1.5 mm long, appressed pubescent on top with simple, several-celled hairs, stigma 2-lobed and impressed beneath by the anthers to assume a 4-lobed appearance. *Fruit* an erect, many-seeded capsule immersed in the chartaceous calyx.

Although attempts have been made to recognize distinct species within the variation displayed by *Browallia americana*, an examination of a wide range of plants from South and Central America shows only slight polymorphism in a single wide-ranging species which grows under considerable diversity of ecological conditions. Characters which vary most noticeably are corolla size, the pubescence, especially its density and its tendency to become glandular or viscid, and a tendency for the calyx lobes to become expanded and sub-foliar at the tips as fruit develops. None of these variations displays a pattern worthy of recognition at the species level. Plants with an especially heavy complement of glandular hairs have been known as *B. viscosa* and may represent a distinct taxon. No other synonyms cited above apply to the glandular form. There is in Panama, at least, however, a seeming altitudinal stratification with respect to flower color. At elevations above about 1,500 m, flowers are mostly very deep blue or purple with a small but conspicuous white eye. From about 1,500 m down to sea level, flowers are mostly violet, mauve or light blue with a white or a white and yellow eye. At about 600 m elevation, one large colony was found with consistently white flowers. These plants have a yellow eye, and upon opening the corolla, the pubescence on the filaments is found to be purplish. This colony is about 2 miles above Paseo la Canoa in Chiriquí Province (*D'Arcy 5314*). Such white-flowered plants may be known as fo. *alba* Stehlé.

Browallia americana occurs throughout Panama, although it is most plentiful at middle and upper elevations, and is infrequent in seasonally dry areas. In the Chiriquí mountains it occurs as an understory herb in forested tracts as well as in the open in pastures, roadsides and other areas of disturbance. "Teresita" (Colombia).

CANAL ZONE: Epiphyte House at lab clearing, Barro Colorado Island, *Croat 5317, 5319, 7964, 10258* (all MO). NW of Pedro Miguel, *Croat 12252* (MO). Balboa Heights, *Greenman & Greenman 5037* (MO). Ancón Hill, *Killip 3020* (US). Barro Colorado Island, *Netting 67, 69* (both MO). Ancon Hill, *Paul 144* (US). Near Ancón, *Piper 6003* (US). Around Culebra, *Pittier 2215* (US). Clearing, Barro Colorado Island, *Shattuck 622* (MO). Moist thicket, Balboa, *Standley 25443* (MO, US). Sosa Hill, *Standley 26407* (C, US). Río Pedro Miguel near East Paraíso, *Standley 29971* (US). Near Summit, *Standley 30126* (US). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1,220 m, *Allen 974* (MO). Near "New Switzerland," central valley of Río Chiriquí Viejo, 1,800–2,000 m, *Allen 1404* (F, MO, US). Ca. 5.4 km del Hato de Volcán en el camino a Las Lagunas, *Correa & Lazor 1510* (MO). Trail N of Cerro Punta, *Croat 10507* (MO). Between Bambito and Cerro Punta, in dense stand of roadside weeds, *Croat 10675* (MO). Near Methodist Camp at Nueva Suisa, *Croat 13534* (MO, NY). Roadside, Nueva California, *D'Arcy 4252*

(MO). Roadside, Los Naranjos, *D'Arcy 4273* (MO). In cafetal beside "Sonrisa Chiricana," Nueva Suisa, Volcán District, 5,700 ft, *D'Arcy 5314* (MO). Very plentiful above Cerro Punta, 6,700 ft, *D'Arcy 5367* (MO). Roadside ca. 2 mi. above Paseo la Canoa, 1,700 ft, *D'Arcy 5426* (G, MO, WIS). Above Boquete, 4,500 ft, *D'Arcy 5442* (MO). Boquete, *D'Arcy 5450* (MO, P, WIS). Scattered plants in pasture, 5,200 ft, La Popa above Boquete, *D'Arcy & D'Arcy 6368* (ADW, BIRM, C, CAL, COI, COL, CORD, DAO, DUKE, F, FSU, G, GH, K, L, LE, M, MO, MPU, NY, P, PMA, POM, PRE, R, TH, UCWI, US, VEN, WIS). Clearing in rain forest, Bajo Chorro, Boquete District, 6,000 ft, *Davidson 357* (MO, US). Valley of Río Chiriquí Viejo N of Volcan City, 5,200–5,600 ft, *Duke 9025* (MO, OS). Cloud forest, Cerro Horqueta, 1,500 m, *Duke et al. 13611* (DUKE, MO, PMA). Boquete, 5,500 ft, *Dwyer 6993* (MO). Finca Collins, Boquete, 5,000 ft, *Dwyer & Hayden 7662* (MO). In recently cleared forest, Fred Collins Finca, Boquete, 7,000 ft, *Ebinger 701* (MO). Near Boquete, 3,300–4,200 ft, *Lewis et al. 341* (MO, US). Audubon cabin in coffee grove, Nueva Suiza, *Partch 69-5* (MO). Pastures around Boquete, 1,000–1,300 ft, *Pittier 2886* (US). Valley of the upper Río Chiriquí Viejo, near Monte Lirio, 1,300–1,900 m, *Seibert 296* (KM, MO, US). Finca Collins, "El Velo," near Boquete 6,150 ft, *Stern et al. 1966* (MO, US). Finca Collins near Boquete, 58–5,700 ft, *Stern et al. 2018* (MO, US). Bambito, 1 mi. SW Cerro Punta, 5,600 ft, *Tyson 5644* (MO). On mountains above Bambito, 1 mi. S Cerro Punta, 6,000 ft, *Tyson 5769* (MO). Río Chiriquí Viejo valley near El Volcán, *White 195* (MO, US). Above Cerro Punta toward Bajo Grande, 6,500 ft, *Wilbur et al. 10925* (DUKE, MO). Roadside woods between Cerro Punta and Bambito, 5,600 ft, *Wilbur et al. 10944* (DUKE, MO). Trailside weed, Paseo de Respinga on way to Boquete, 7,500 ft, *Wilbur & Teeri 13186* (DUKE). Weed in cornfield between Cerro Punta and Las Nubes on eastern side of Cerro Punta (mountain), *Wilbur & Teeri 13245* (DUKE). Trailside, Río Caldera beyond Bajo Mono ca. 4 mi. NW of Boquete, 4,200 ft, *Wilbur et al. 13504* (DUKE). Vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson 855* (MO). COCLÉ: Mountains N of El Valle de Antón, cloud forest, 2,500–3,000 ft, *Lewis et al. 1782* (MIN, MO, UMO, WAG). Edge of cloud forest and roadside, El Valle de Antón, 1,000–2,000 ft, *Lewis et al. 2559* (MO). DARIÉN: Along gravel bars on river between Río Perecenico and Rancho Frio, 500–2,500 ft, *Duke & Elias 13863* (DAO, MO, W). Near Campamento Buena Vista Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 841* (MO, US). PANAMÁ: Taboga Island, up to 300 m, *Allen 107* (K, MO), *140* (MO). Without locality, *Cuming 1195* (BM). A few plants about halfway up mountain, Cerro Campana, *D'Arcy & Dressler 5502* (GH, MO, NY, WIS). Along Pan-Am Highway, open grazed area near Jenine, Río Cañita, *Duke 3823* (MO US), *3839* (MO). Río Charco-Espiritu on Tocumen Highway, "chavelita de monte," *Duke 5695* (MO). Near El Llano, *Duke 5852* (H, MO). Bald savanna-like areas along road toward top of Cerro Campana, *Duke 5992* (MEXU, MO). Dam site near Río Bayano beyond, Cañita, *Gentry & Tyson 1684* (MO). *Halsted s.n., 1850* (NY). Capira, *Maurice 801* (US). Capira, *Paul 122* (US). Sabanas, *Paul 231* (US). Without locality, *Seeman*, Apr. 1837 (K), *s.n.* (BM). Taboga Island, *Standley 27086* (US), *27930* (C, US).

B. Section **Leiogyne** Miers, Ann. Mag. Nat. Hist., ser. 2. 5: 207. 1850. TYPE: *B. speciosa* Hook.

2. **Browallia speciosa** Hook., Bot. Mag. *Tab. 4339*. 1947. TYPE (not seen).— FIG. 1.

B. gigantea Mörner, Svensk. Linné-Sällsk. Arssk. 17: 21, 1934, nomen nudum.

Erect or sprawling *herb* to 70 cm tall; stems puberulent with short, simple, mostly forward-directed hairs. *Leaves* ovate or elliptic, to 6 (–9) cm long, acuminate apically, short acuminate or obtuse basally, margins entire or nearly so, somewhat upfolded at the petiole, above with scattered simple hairs on the lamina, beneath puberulent on the veins, petiole ca. ¼ as long as the leaves. *Pedicels* glabrous ca. 7 mm long but elongating (3–4 cm) in fruit. *Flowers* showy, the calyx 5–10 mm long with a few hairs on the angles, the tube inflated to appear bladder-like with 5 prominent angles, lobed ⅓ the way down, the

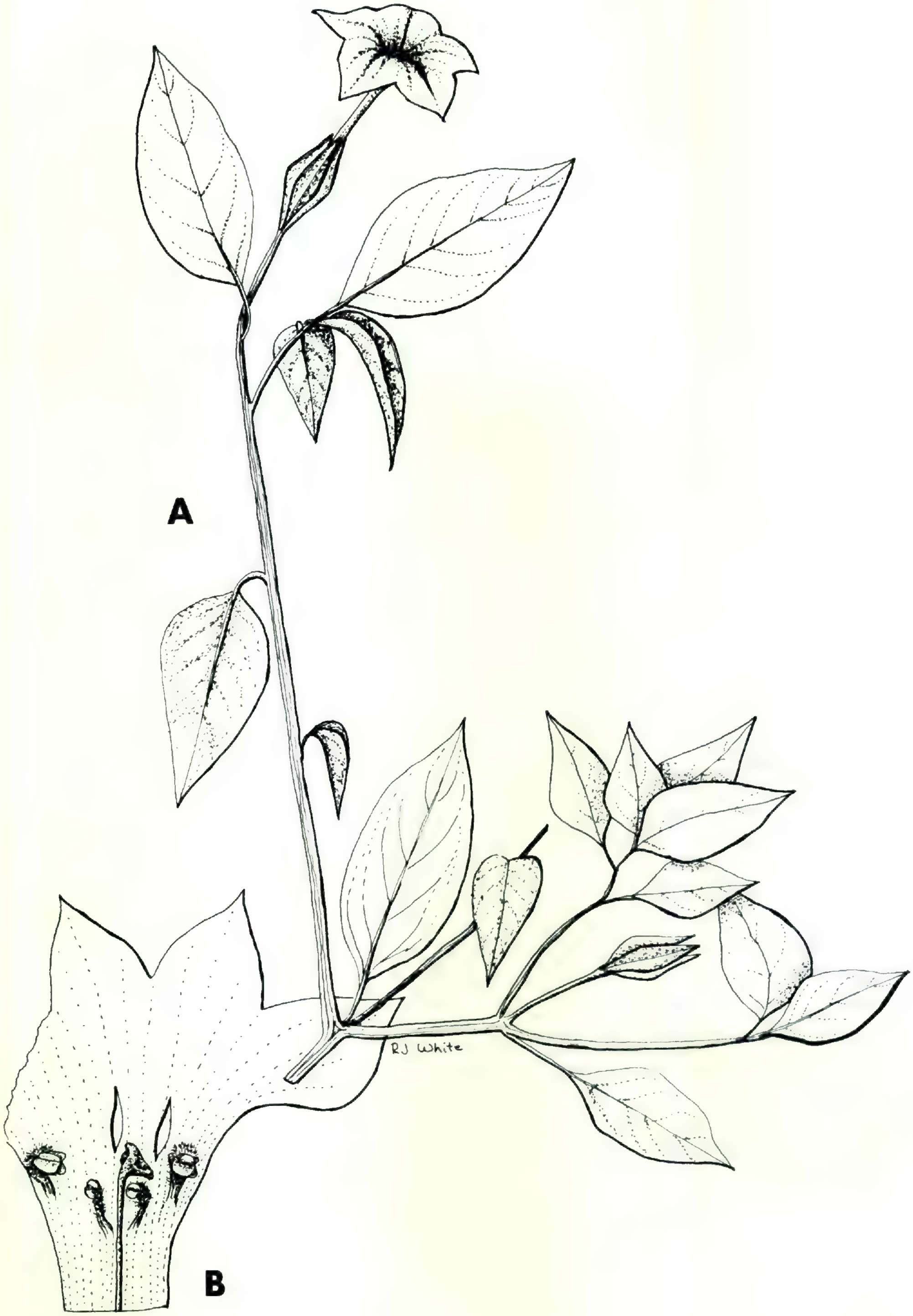

FIGURE 1. *Browallia speciosa* Hook.—A. Flowering branch ($\times$ ⅔). [After *Allen 4790* (MO).]—B. Opened flower showing androecium and top of gynoecium ($\times$ 1⅓). [After living material cultivated from seed purchased in North America, *D'Arcy 7156* (MO).]

lobes acuminate-deltoid and directed inward against the corolla tube; corolla blue, mauve or white, salverform, often with an irregular-margined white eye, the tube 20–50 mm across, glabrous within, dorsally puberulent with short, erect, several-celled, often pigmented glandular hairs, their terminal cell transparent and acicular (bayonet hairs); stamens 4(–5) usually with a staminode, the filaments of the upper pair green, apically pilose with long, dense, colored dendritic hairs, the shorter two with terete filaments, anthers yellow or purplish, ovary glabrous, slightly angled, 3 mm long. *Capsule* becoming 2 cm across, immersed in the coriaceous calyx.

This species is best recognized by its large, showy flowers which on drying have sharply pointed lobes. Few collections have been seen from Panama. For the above description, seed from temperate seed houses was grown for examination and the plants used to ascertain features within the corolla tube and of the fruit.

CHIRIQUÍ: Very common trailside herb, Bajo Mono–Robalo Trail, W slope of Cerro Horqueta, 5,000–7,000 ft, *Allen 4790* (K, MO). Dense humid forest, valley of the Río Caldera from El Boquete to the Cordillera, 1,400–1,600 m, *Killip 3560* (MO). Humid forest along upper Caldera River, Holcomb's trail above El Boquete, 1,450–1,650 m, *Maxon 5603* (F). Cloud forest, Cerro Horqueta 6,500 ft, *von Hagen & von Hagen 2099* (MO).

2. BRUGMANSIA

Brugmansia Pers., Syn. Pl. 1: 216. 1805, non Blume *in* Van Hall, Bijdr. Natuurk. Wetensch. 2: 422. 1828, Rafflesiaceae. TYPE: *B. candida* Pers.

Pseudodatura Van Zijp, Natuurk. Tijdshr. Ned.-Indië 80: 24–28. 1920. TYPE: Not designated.
Methysticodendron R. E. Schultes, Bot. Mus. Leafl. 17: 2. 1955. TYPE: *M. amesianum* R. E. Schultes.

Unarmed *trees* or *shrubs*, pubescence of mostly simple, sometimes viscid hairs; twigs mostly stout. *Leaves* simple and entire or repand, petiolate, mostly large. *Flowers* solitary (sometimes aggregated) on erect or pendulous pedicels, showy, mostly 5-merous; calyx tubular, sometimes inflated or strongly angled and sometimes appressed to the corolla tube, prefloration complete and floral egress by 5 or more valvate teeth usually dehiscing irregularly to form one or more spathaceous lobes; corolla funnelform, tubiform or almost tubular, mostly large, variously colored, flaccid and succulent, glabrous or variously pubescent, the limb sinuate margined or 5-toothed, sometimes opening or scented nocturnally; stamens equal, the filaments inserted near the top of the tube, sometimes geniculate, variously pubescent, the anthers linear, basifixed, dehiscing longitudinally, coherent or free; ovary conical, 2-loculed with many ovules on an enlarged placenta, the stigma elongate and exceeding the anthers, the stigma variously shaped but mostly small and 2-lobed. *Fruit* an unarmed, spheroidal or elongate, woody, indehiscent capsule, seeds large and wedge shaped, embryo straight in fleshy endosperm.

This genus was long considered conspecific with *Datura* to which it is closely related. The arboreal habit, unarmed fruits and 2-loculed ovaries are significant differences. This group is under study by Dr. T. E. Lockwood of Illinois University.

Brugmansia includes about 15 species centered in northwestern South America. These are plants of cultivation and truly wild populations may not exist. As important medicinal and ritual subjects for man, they have been transported far from their presumed native regions. Several species are now widely cultivated in tropical regions and greenhouses in both New and Old worlds.

In Panama, *Brugmansia* species are grown only for ornament or fence posts and they are a welcome ornamental to the rural homestead. Plants are commonly propagated by vegetative means and no fruiting material is known from Panama. Many species in the genus are self-sterile and the absence of fruit may be a consequence of very few introductions of the genus to Panama.

Brugmansia takes its name from Sebald Justin Brügmans, (1763–1819) professor of natural history and the botany of Batavia at Leiden.

Useful references:

Bristol, M. L. Tree *Datura* drugs of the Colombian Sibundoy. Bot. Mus. Leafl. 22(5): 165–227. 1969.

Lockwood, T. E. Generic recognition of *Brugmansia*. Bot. Mus. Leafl. 23(6): 273–283. 1973.

Safford, W. D. 1921. Synopsis of the genus *Datura*. Jour. Washington Acad. Sci. 11: 173–189.

a. Calyx glabrous outside; width of corolla tube nearly filling the calyx mouth; corolla teeth ca. 30 mm long; calyx mostly once cleft; anthers free, 22–23 mm long; corolla white ---------- 1. *B. candida*

aa. Calyx pubescent outside; width of corolla tube less than ⅔ the diameter of the calyx mouth; corolla teeth 10–15 mm long; calyx 5-cleft or lobed; anthers coherent (sometimes ultimately separating), 25–35 mm long; corolla white or colored ---------- 2. *B. suaveolens*

1. **Brugmansia candida** Pers., Syn. Pl. 1: 216. 1805. TYPE: Based on *Datura arborea* R. & P.—FIG. 2.

Datura arborea R. & P., Fl. Peru. 2: 15, *tab. 127*. 1799, non L., Sp. Pl. 191. 1953, nec Lagerh., Bot. Jahrb. Syst. 20: 663. 1895. TYPE: Peru, *Pavon s.n.* (MO, lectotype; B-W, isolectotype, not seen, IDC 7740 [7440 sic.] 293 II: 9 (herb. Willd.)).
D. candida (Pers.) Safford, Jour. Washington Acad. Sci. 11: 182–3. 1921.

Shrub or *tree* to 5 m tall; twigs stout, green, puberulent with ascending hairs. *Leaves* ovate or elliptical to 25 cm long, the apex acute, the base rounded or obtuse, mostly dimidiate, puberulent on the lamina above and with scattered short hairs beneath; petioles 3–8 cm long, puberulent. *Pedicels* to 4 cm long, erect in bud, soon pendulous and becoming more slender during elongation. *Flowers* very large, calyx sparingly fine puberulent outside, inflated in bud, becoming ± narrowly tubular and 10–12 cm long by anthesis, the apex mostly once cleft, spathaceous, the cleavage extending ca. ⅓ the way down the calyx; corolla white, sometimes with a greenish cast, 25–30 cm long, pendant, tubiform and flaring widely at the limb, the tube mostly filling the calyx tube, the limb sinuate lobed, ca. 15 cm across with five lanceolate teeth ca. 30 mm long, puberulent on the ribs outside, glabrous within; filaments inserted slightly below the middle of the corolla (level with the top of the calyx), 37–38 mm long, free, geniculate,

FIGURE 2. *Brugmansia candida* Pers., opened flower (× 3/5). [After *D'Arcy* 5308 (MO).]

pilose near the point of insertion, glabrous above, elevated and broadened below, anthers 22–23 mm long, narrowly elongate, slightly hastate basally and emarginate apically, at first coherent but ultimately separating, pilose on the sutures; ovary green, narrowly conical, 10–15 mm long, the style slender and broadening slightly above the anther tube, the stigma with 2 distinct but flattened, obtuse lobes ca. 4 mm long, stigmatic on their edges. *Fruit* (Ruiz & Pavon) a smooth, elliptical, indehiscent capsule, the two locules marked off by shallow, longitudinal depressions on the outside and the many seeds shaped like reniform wedges (not known from Panama).

This is the common "floripondio" of the Chiriquí mountain villages. It is one of the most frequent and striking plants in the region, used as a specimen tree and in hedges, as fence posts and sometimes forming thickets where it roots from trash.

Brugmansia candida is not known outside of cultivation except for spontaneously rooting plants in districts where it is cultivated. It is widespread in rural areas in tropical America and is cultivated in parts of the Old World. It may be native to Peru.

Of incidental interest are the fruit flies (*Drosophila*) which inhabit the corollas of this species. Flies gather within the corollas soon after they open. Occurring in the area proximal to the anthers, they do not seem to act in pollination. Fallen blossoms take several days to decompose and they often contain *Drosophila*-like larvae. It may be that these fruit flies complete their life cycle in association with *Brugmansia candida*. Dr. Hampton Carson, University of Hawaii, has stated (personal communication) that these species of *Drosophila* have been found only in association with *Brugmansia*.

CHIRIQUÍ: Cerro Punta, 6,500 ft, *Blaisdell 355* (FSU). Alto Boquete along main road, cultivated, *Correa 428* (MO, PMA). Near Bambito, roadside, *Croat 10613* (SCZ). Nueva California, planted by fence, *D'Arcy 4248* (MO.) Nueva Suisa, Volcan District, 5,700 ft, *D'Arcy 5308* (MO, MPU). Cerro Horqueta, ca. 4,500–5,500 m, rain forest, *Dwyer 8732* (MO). Bambito, 1 mi. SW Cerro Punta, 5,600 ft, ornamental, *Tyson 5754* (BISH, FSU, MO). PANAMÁ: Without locality, *Halsted*, 1850 (NY).

2. **Brugmansia suaveolens** (Willd.) Sweet, Hort, Brit., ed. 3: 506. 1839.

Datura suaveolens H. & B. *ex* Willd., Enum. Hort. Berol. 227. 1809. TYPE: *Humboldt s.n.* (B-W, not seen; IDC 7740 [7440 sic.] 14 III: 1, 2 (Herb. Willd.)).

Shrub or tree to 5 m tall, twigs glabrous or puberulent. *Leaves* ovate, apically acute or acuminate, basally rounded or obtuse, dimidiate, puberulent to pilose on both sides and especially along the veins; petioles 3–5 cm long, glabrate. *Pedicels* to 5 cm long, glabrate or pubescent. *Flowers* very large and showy; the calyx broadly tubular, inflated in bud and remaining so in flower, falling in entirety with the corolla, apically 5-lobed, the lobes equal, obtuse or acute, 2–3 cm long, glabrate or pubescent; corolla white, pink or yellowish, 25–30 cm long, pendant, tubiform, sometimes with a slight expansion about halfway along the limb, the tube less than ⅔ the diameter of the calyx tube (not nearly filling it), the limb sinuate lobed, ca. 13 cm across with five narrowly lanceolate teeth 10–15 mm long, pubescent outside glabrous within; the filaments geniculate

or not, inserted ⅓–½ of the way up the corolla (above the top of the calyx), pilose near the point of insertion, glabrous and sometimes drying dark above, ca. 40 mm free, the anthers 25–35 mm long, coherent into a narrow, cyclindrical tube 4–6 mm across, sometimes ultimately separating, dehiscing longitudinally, the sutures appearing pilose; ovary elongate-conical. *Fruit* not known in Panama.

Brugmansia suaveolens, especially white flowered forms, is like *B. candida* in general appearance and is frequently confused with it in the herbarium. The calyx teeth, corolla pubescence, anther length and especially the narrow corolla tube in a large calyx mouth are good diagnostic characters.

Both white and pink flowered forms have been collected in Panama. The white form is known only from two collections (*Lewis et al. 1757* and *Hayes 101*). In the Volcán district of Chiriquí the pink form has recently become plentiful, and is being used as an ornamental and for fenceposts in much the same way as *B. candida*. It may be a recent introduction as householders do not remember seeing it before 1966 or 1968. Flowers in the Hato de Volcán to Nueva California district must be seen in the morning, as by about 11:00 a.m. most of the flowers close by rolling up the limb, and they then take on a greenish or yellowish appearance. Plants seen near Nueva Suisa, however, ca. 300 m higher (ca. 2,000 m) remain open all day.

CHIRIQUÍ: Common in town of Los Naranjos, cultivated, *D'Arcy 4272* (MO). Nueva Suisa, Volcán District, 6,000 ft, *D'Arcy 5417* (MO). PANAMÁ: Aspinwall, *Hayes 101* (NY). El Valle de Antón, cloud forest, 2,500–3,000 ft, *Lewis et al. 1757* (MO).

3. BRUNFELSIA

Brunfelsia [Plum.] L., Sp. Pl. 191. 1753; Gen. Pl., ed. 5. 87. 1754. TYPE: *B. americana* L.

[*Brunfelsia* Plum., Nov. Pl. Amer. Gen. 12, *tab.* 22. 1703].
Franciscea Pohl, Pl. Bras. Ic. 1: 1, *tab. 1–17*. 1827. TYPE: Not designated.
Martia J. A. Schmidt *in* Mart., Fl. Bras. 8(1): 261. 1862, nomen nudum, non *Martia* Spreng., Anleit. II 2: 788. 1818, Hypericaceae.
Brunfelsiopsis Urb., Notizbl. Königl. Bot. Gart. Berlin 1: 324–325. 1897. TYPE: *Brunfelsia densifolia* Krug. & Urb.

Unarmed *shrubs* or *trees*, glabrous or with simple hairs; twigs sometimes angled. *Leaves* entire, coriaceous to chartaceous, often glabrate, sometimes appearing clustered at the ends of twigs; petioles mostly short; minor leaves wanting. *Flowers* solitary or clustered, appearing terminal, sometimes bracteate; calyx tubular to cyathiform, 5-lobed, in fruit slightly accrescent, coriaceous and splitting along one or more sides; corolla showy blue, purple or white, often fading to white or yellow, salverform, quincuncial in bud, slightly zygomorphic, the lobes rotund; stamens 5, 1 or more reduced to staminodes or wanting, didynamous, the filaments straight or slightly curved apically, often tumid near the apex, inserted along the length of the corolla tube, the anthers included; ovary ovoid on a short stipe, 2-loculed, but 1-loculed apically with many axile ovules, the stigma capitate, sometimes incurved. *Fruit* a globose to ovoid fleshy or coriaceous, mostly indehiscent berry; seeds large, prismatic, the embryo straight or slightly curved in fleshy endosperm.

A genus of 25–30 species of tropical America, several widely cultivated for ornament. The floral characteristics are similar to those of *Browallia* and other genera of the Salpiglossidae. This is the only American genus in the tribe which is not herbaceous.

The genus was named in honor of Otto Brunfels, 1489–1534, a German botanist. Species are usually known in Spanish as "galan de noche."

Mr. Timothy Plowman of Harvard University is currently studying *Brunfelsia* with a view to preparing a monograph of the genus.

a. Corolla tube less than 5 cm long, limb (including lobes) at least half as wide as the tube length; fruit maturing in Panama; forest species.
  b. Corolla limb more than 5 cm across; mature fruit green or brown, hard ..... 2. *B. dwyeri*
  bb. Corolla limb less than 4 cm across; mature fruit yellow, fleshy ..... 1. *B. chocoensis*
aa. Corolla tube more than 5 cm long, limb (including lobes) less than half as wide as the tube length; fruit not setting in Panama, cultivated species ..... 3. *B. undulata*

1. **Brunfelsia chocoensis** Plowman, Bot. Mus. Leafl. 23(6): 245. 1973. TYPE: Colombia, *Haught 4563* (UC, not seen).

Shrub 2 m tall, twigs terete, the bark flaking in scales which gives a puberulent appearance to the naked eye. *Leaves* obovate or elliptical, basally obtuse, apically acuminate, veins ca. 4 on each side of the midrib, membranaceous, glabrous. *Inflorescence* of solitary, flowers. *Flowers* fragrant (Bristan), the calyx tubular campanulate, glabrous, longitudinally striate, reticulate, the lobes 2–4 mm long, enlarging to 13 mm long in fruit and becoming lenticel-dotted; corolla white, the tube twice as long as the calyx, 22–27 mm long and 2–2.5 mm broad, glabrous, the limb salverform, 2–2.5 cm across, the lobes subequal, 8–10 mm long; stamens included, inserted in the upper ⅓ of the corolla tube, the anthers 2 mm long, reniform-hippocrepiform, light brown; ovary glabrous, 2.5 mm long, the style slender, the stigma bifid, with lobes 1.5 mm long, oblong. *Fruit* a yellow, smooth, fleshy, globose to ovoid berry 2–3 cm across; seeds 2–5, ovoid-ellipsoid, angular, 8–10 mm long, 6–7 mm in diameter, dark brown.

This species is distinctive in its fleshy, yellow fruit, small white flowers and large leaves, which have been reported as long as 28 cm. The Panamanian material is fragmentary so the above description is taken mainly from that of Plowman.

The species is known only from eastern Panama and the Choco region of Colombia.

DARIÉN: Cerro Pirre, *Bristan 569* (OS).

2. **Brunfelsia dwyeri** D'Arcy, Ann. Missouri Bot. Gard. 57: 259. 1970. TYPE: Panama, *Tyson et al. 3312* (MO-1820936, holotype; MO, isotype).

Slender, glabrous *tree* to 10 m tall; bark grey-white, flaking; twigs often appearing angled or flattened. *Leaves* coriaceous, elliptic to slightly oblanceolate, mostly 4–10 cm long and 1.5–4.5 cm broad, acuminate at the apex, acute at the base with entire margins, the lamina upfolded from the somewhat recurved

midrib; petioles 3 (rarely 12) mm long, channeled above. *Inflorescence* of solitary, axillary, almost terminal flowers; the peduncle to 6 mm long, often (especially in fruit) almost absent, bearing several scalelike bracts; pedicels glabrous, 5–15 mm long, broadening gradually upwards. *Flowers* showy, calyx yellow, ellipsoidal, appearing tubular when dried, ca. 15 mm long, often conspicuously striate-verrucose with corky excrescences, coriaceous, the lobes obtuse, ca. 4 mm long, converging on the corolla tube, the entire calyx enlarging somewhat and splitting at one or more sinuses in fruit; corolla very showy, deep purple fading to white before falling but maintaining a small yellow eye, tube 3–4 cm long and 3–4 mm broad, slightly curved, the limb salverform, 3–4 cm across plus the 5, orbicular lobes, 2.5 cm long; stamens included, the filaments glabrous, inserted in the upper part of the corolla tube, the anthers small, crescent shaped, 1-thecate; ovary glabrous, ca. 1.5 mm long, the style glabrous, the stigma with 2 unequal discoid lobes. *Fruit* a leathery, dark greenish-brown, globose-ovoid berry, usually warty, 1.5–2.5 cm across, the apex usually crossed by a pair of sutures; seeds many, prismatic, 9 mm long, with a soft thick translucent testa which drys reddish brown.

Brunfelsia dwyeri is an occasional tree in the disappearing forests on Cerro Jefe and Cerro Azul, Province of Panamá. The species has a showy purple flower color.

PANAMÁ: Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 471* (MO, PMA). Region of Cerro Jefe, ca. 1,000 m, edge of forest, *Correa et al. 1599* (MO, PMA). Cerro Jefe along main road before turnoff to summit, *Croat 13036* (MO). Along main road past Cerro Jefe toward La Eneida, *Croat 13072* (MO). Cerro Jefe, *D'Arcy 3948, 3959* (both MO); *Duke 9429* (MO). Secondary cloud forest, summit of Cerro Jefe, *Dwyer et al. 5551* (MO). Cerro Jefe, *Dwyer et al. 7280* (MO). Forest edge and road bank, Cerro Jefe, 2,900 ft, *Dwyer & Gauger 7349* (MO). Cerro Azul-La Eneida growing along roadsides, *Escobar 359* (ECON). Cerro Jefe 10 mi. from Tocumen Circle, *Gentry 2876* (MO). Cerro Jefe along road to La Eneida ca. 5 km past Goofy Lake, *Kennedy 316* (ECON). On road to Cerro Azul (La Eneida) 5.40 km past Goofy Lake, common, in old secondary forest along roadside, not cultivated, *Kennedy 352* (ECON). Along road from Cerro Azul to Cerro Jefe at 2,300–2,700 ft, *Tyson et al. 3312* (MO, PMA), *4335* (DUKE, MO); *Tyson 5313* (MO). Above Goofy Lake ca. 8 km on road to Cerro Jefe, *Weaver & Foster 1497* (DUKE). Forested slopes of Cerro Jefe near large coffee finca, *Wilbur et al. 11319* (DUKE). Slopes of Cerro Jefe beyond Cerro Azul, *Wilbur & Teeri 11358* (DUKE, MO).

3. **Brunfelsia undulata** SW., Flor. Ind. Occ. 90. 1797. LECTOTYPE: Jamaica, *Swartz s.n.* (S).—FIG. 3.

B. americana sensu hort., non L., Sp. Pl. 191. 1753.

Glabrous *shrub* or *tree* to 5 m tall. *Leaves* narrowly elliptic to oblanceolate, mostly 8–10 cm long, acute or acuminate apically, acute basally, the margins entire and sometimes slightly revolute; petioles less than 4 mm long, channelled above and often verrucose. *Inflorescence* a cluster of solitary, subterminal flowers, each sometimes subtended by a pair of foliaceous bracts 1–4 cm long;

→

FIGURE 3. *Brunfelsia undulata* SW., flowering branch (× 7/10). [After *D'Arcy & Croat 4201* (MO).]

RJ White

peduncle very short or wanting; pedicels 8–12 mm long. *Flowers* showy, calyx cyathiform, ca. 10 mm long, the lobes orbicular, 3–4 mm long; corolla white fading to yellow, sometimes with a small, brownish-purple eye, the tube slender, ca. 10 mm long and 2–3 mm across, pubescent in the lower half within, the limb ca. 1.5 cm across plus the 5, orbicular lobes, 10–15 mm long; filaments pubescent near the point of insertion and below, the anthers narrowly elliptic; stigma semilunar, green. *Fruit* not known in Panama.

In Panama this species is known only in cultivation. It is a common ornamental shrub in lowland Panama, especially in rural areas of seasonal rainfall. As a dooryard plant it is much esteemed both for the showy appearance of the flowers and for the far-reaching nocturnal scent. "Galan de noche."

LOS SANTOS: Cultivated in Pocrí, *D'Arcy & Croat 4201* (MO). PANAMÁ: Chepo, flowers showy white, fading yellow, shrub 3 m tall, cultivated, very plentiful in yards in this town, *D'Arcy 3944* (MO).

4. CAPSICUM

Capsicum L., Sp. Pl. 188–9. 1753; Gen. Pl., ed. 5. 86. 1754. TYPE: *C. annum* L.

Erect or clambering short-lived perennial *herbs*; stems sometimes angled, glabrous or pubescent with simple, sometimes glandular hairs. *Leaves* simple, entire or weakly toothed, mostly ovate or elliptical; abruptly or gradually narrowed into a slightly winged petiole; minor leaves present or not. *Inflorescence* one or a few flowers fascicled in the leaf axil; the flowering pedicels mostly downward curved, erect or curved in fruit, sometimes angled. *Flowers* with the calyx cyathiform or short tubular, truncate or with 5 or 10 short teeth, sometimes accrescent but not enclosing the fruit, rarely with an annular thickening or ferrule around the base; the corolla small, yellow, white or bluish, sometimes spotted, deeply lobed; the stamens 5, equal, the filaments inserted at the base of the corolla tube, the anthers yellow or purple, dehiscing longitudinally; the ovary glabrous, 2-loculed, many-ovuled, the stigma puntiform or capitate. *Fruit* a dry, coriaceous to fleshy berry with large air spaces in the locules, bright purple, red, orange, yellow or white, comestible. *Seeds* flattened-lenticular, yellow (Panama), small; embryo curved around the periphery of the seed; the endosperm fleshy.

A genus of perhaps a dozen species, many of them grown for their culinary and ornamental fruits. For many years this genus was confused with *Witheringia*, which differs in its often woody habit, apiculate anthers, and juicy fruits. *Capsicum* has a close relationship with *Lycianthes*, for the calyx teeth, when present, are secondarily derived in much the same way. In Panama, as well as in other tropical American countries, there is frequent hybridization between large-fruited horticultural strains and the small-fruited, bird dispersed, wild strains, the result being many plants with intermediate characteristics, especially near human habitation.

The name is perhaps from the Latin "cirpsa" = capsule, although the fruit is a berry. "Aji," "peppers" (English).

Useful reference:

D'Arcy, W. G. & W. H. Eshbaugh. New World peppers north of Colombia: A resumé. Baileya 19: 93–105. 1974.

a. Pedicels after first flowering node mostly one to a node; prominent constriction lacking between the base of the calyx and the pedicel; corolla pure white to bluish white.
  b. Fruits large, mostly more than 1 cm across ..... 1a. *C. annuum* var. *annuum*
  bb. Fruits small, mostly less than 1 cm across ..... 1b. *C. annuum* var. *aviculare*
aa. Pedicels mostly 2 or more per node (look for scars); prominent constriction sometimes present between the base of the calyx and the pedicel; corolla dull white or greenish white.
  c. Constriction absent between base of calyx and pedicel; corolla greenish white; fruit usually erect, deciduous, soft fleshed; style exserted 1.5 mm or more beyond the anthers ..... 3. *C. frutescens*
  cc. Constriction present between the base of the calyx and pedicel; corolla dull white; fruit usually pendant, persistent, firm fleshed; style exserted 1 mm or less beyond the anthers ..... 2. *C. chinense*

1. **Capsicum annuum** L., Sp. Pl. 188. 1753. LECTOTYPE: *Hort. Cliff.* 59 (BM).

1a. **Capsicum annuum** L. var. **annuum**

Herb or small *shrub* to 1.5 m tall, short-lived perennial or cultivated as an annual, mostly glabrate. *Leaves* mostly ovate, subentire, to 15 cm long; petioles often elongate. *Flowers* mostly solitary, rarely in pairs; pedicels slender to very thick, often enlarging in the distal portion; calyx truncate or with umbos less than 0.5 mm long, constricted at the base only tardily under stress of the enlarging fruit; corolla white, rarely with a bluish hue, mostly lacking yellow, green or brown markings, lobed about halfway, the lobes obtuse and about as long as broad; the anthers more-or-less violet, sometimes drying green, the filaments short. Fruit extremely variable as to size, shape, color and flavor.

This is the most widespread species of *Capsicum* and it is probably cultivated in every country in the world. In Panama it is widely cultivated as a dooryard crop and sometimes commercially.

Variety *annuum* is considered to embrace the cultivated plants of the species which usually have larger flowers and fruits than the wild plants. In towns and near dwellings in the countryside, intermediates are to be found.

CANAL ZONE: Gamboa, *Standley 28523* (US). Río Paraíso above East Paraíso, *Standley 29880* (US). Frijoles, *Standley 31479* (US). Barro Colorado Island, *D'Arcy 5508* (MO); *Croat 6252, 6683, 9007* (all MO). PANAMÁ: Weed behind cantina, Cañita, *D'Arcy 5187* (MO).

1b. **Capsicum annuum** var. **aviculare** (Dierb.) D'Arcy & Eshbaugh, Phylologia. 25: 350. 1973.[6]—FIG. 4.

C. conoide Mill., Gard. Dict., ed. 8. 8. 1768. TYPE: (not seen).
C. indicum 5. *microcarpon* var. *aviculare* Dierb., Handb. Med-pharm. Bot. 28. 1819. TYPE: Based on *C. conoide* Mill.
C. annuum var. *baccatum* (L.) O. Kuntze, Rev. Gen. Plant. 449. 1891, non L.
C. annuum var. *minus* (Fingerh.) Shinners, Baileya 4: 82. 1956, non Fingerh.
C. annuum var. *minimum* (Mill.) Heiser, Ci. & Nat. 7: 52. 1964.

[6] For a list of synonyms see D'Arcy and Eshbaugh (1974: 99). Only the names listed here have been applied to Panamanian material.

Herb or small *shrub* mostly to 2 m tall but sometimes high climbing, mostly a short-lived perennial but sometimes persisting longer, mostly glabrate. *Leaves* ovate, to 10 cm long, glabrate, the petiole slightly winged, slender, less than ⅓ as long as the leaves. *Flowers* mostly solitary; the pedicels slender, often longer than the petioles, enlarging slightly near the fruit; calyx mostly truncate or with small umbos in the place of teeth; corolla white, rarely greenish, ca. 8 mm across, deeply lobed; the anthers violet, the filaments less than 1 mm long; the ovary glabrous. *Fruit* mostly erect on elongating pedicels, globose, ovoid or elongate-conical, to 3 cm long and 9 mm wide, red or orange, deciduous, hot to the taste.

This is the common American bird pepper, found from the southern United States to northern South America and widespread in the Antilles. It is frequent in Panama at low and middle elevations as a weed of fence rows, pastures, cafetales, and waste places. In towns, the pepper which occurs as a street weed usually has larger flowers and fruits, probably a product of hybridization between var. *aviculare* and var. *annuum*.

BOCAS DEL TORO: Zigla road at junction of Río Changuinola and Río Tuibe, *Lazor et al. 2525* (FSU). CANAL ZONE: Near Madden Dam, *Allen 2006* (MO, US). High climbing in trees (4 m) in shade of Río Coco Solo Bridge, Transisthmian Highway, *D'Arcy 5170* (MO). Causeway, Fort Amador, *Dwyer 2559* (US). Near Gatuncillo, *Piper 5648* (US). Mamei Hill, *Pittier 3810* (US). Las Cascadas Plantation near Summit, *Standley 25825, 29640* (both US). Darién Station, *Standley 31543* (US). N of Summit Garden 1 mi., *Tyson & Blum 1946* (FSU, MO). CHIRIQUÍ: Near Puerto Armuelles, *Woodson & Schery 840* (US). COCLÉ: 10 mi. E of Nata at Río Grande, *Tyson 5214* (FSU, SCZ), *5222* (FSU, MO). DARIÉN: Near Río Chucunaque and mouths of Río Canglón and Río Tuquesa, *Sexton 219* (MO). Near El Real, Río Tuira, *Stern et al. 798* (US). Without locality, *Tyson et al. 4674* (FSU, SCZ). Boca de Cupe, *Williams 715* (US). LOS SANTOS: Near headwaters of Río Pedregal, 25 mi. SW of Tonosí, 2,500–3,000 ft, *Lewis et al. 2939* (MO). Guayabo, a place several mi. W of Tonosí, *Stern et al. 1901* (US). One mi. N of Tonosí, *Tyson et al. 2989* (MO, SCZ). PANAMÁ: Near Río Bayano dam ca. 5 mi. S of Cañita, *D'Arcy 5195* (MO). Dam site near Río Bayano beyond Cañita, *Gentry & Tyson 1680* (ADW, MO, MPU). Las Sabanas, *Standley 25887* (US). Río Tocumen, *Standley 29336* (US). Juan Diaz, *Standley 30539* (US). Between Las Sabanas and Matias Herandez, *Standley 31921* (US). Taboga Island, near village, *Tyson 5588* (FSU, SCZ). SAN BLAS: Above Puerto Obaldía, *Gentry 1532* (MO). Forests around Puerto Obaldía, *Pittier 4299* (US).

2. **Capsicum chinense** Jacq., Hort. Bot. Vindob. 3: 38, *tab. 67*. 1776. TYPE: (not seen).

Small, short lived *shrub* to 1.5 m tall, glabrate or puberulent. *Flowers* mostly 2–5 per node; pedicels recurving and becoming thick in fruit; calyx with a pronounced constriction between the base of the calyx and pedicel, teeth mostly absent; corolla dull white or somewhat greenish; the lobes spreading to recurved; anthers blue to violet, rarely yellow; the stigma not exserted from the anthers more than 1 mm. *Fruit* pendant, persistent, variously shaped, but often with longitudinal furrows, the fruit wall fleshy, ripening brown, red, orange, pink, yellow or almost white; seeds cream to yellow.

Capsicum chinense is cultivated from the southern United States to Chile. Negro populations in the Caribbean area commonly grow it for use in soups and stews. In some strains from the Antilles or the Portobelo region of Panama, the fruit resembles a miniature, shiny plastic replica of the fruit of *Hura*

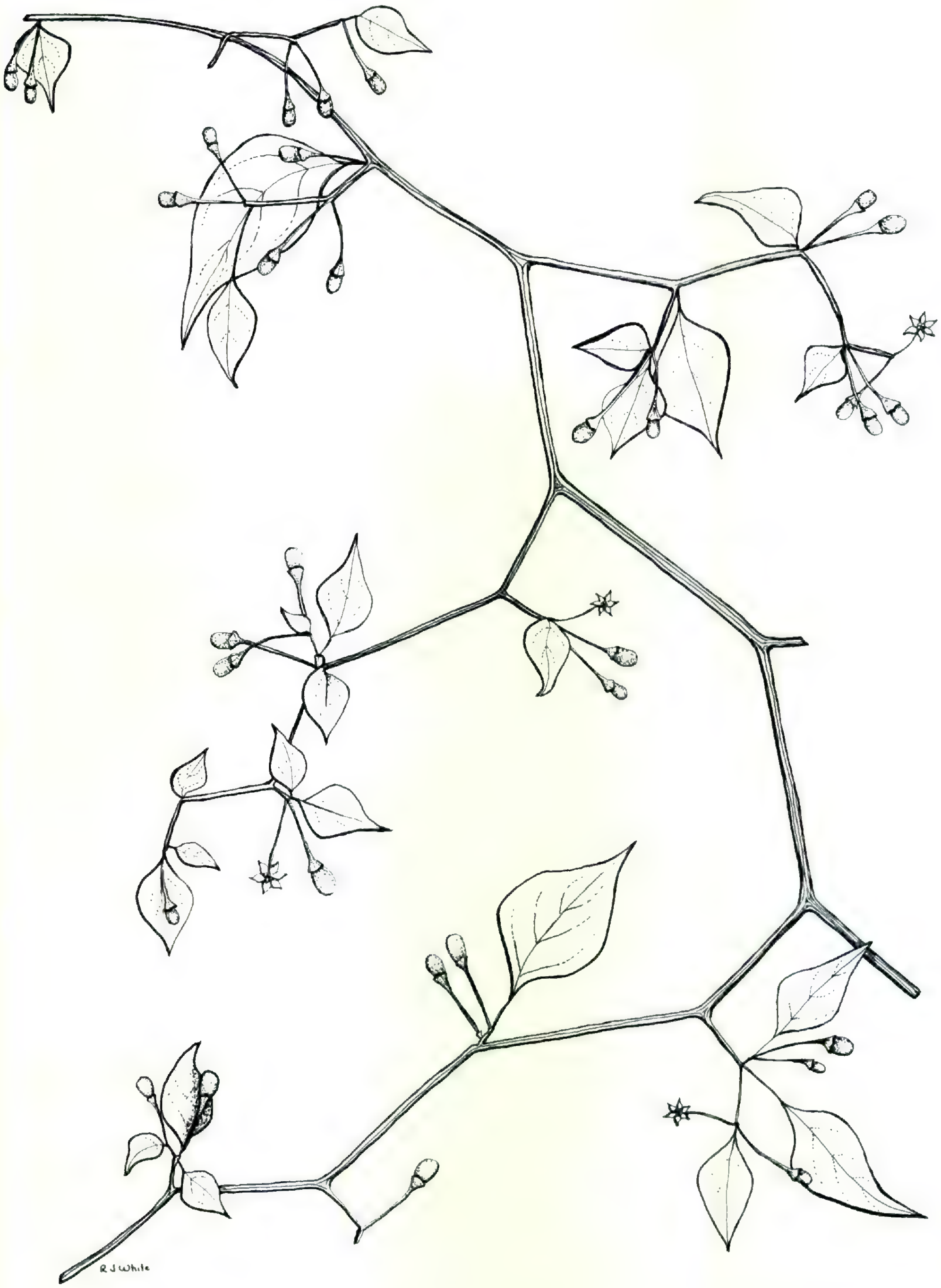

FIGURE 4. *Capsicum annuum* var. *aviculare* (Dierb.) D'Arcy & Eshbaugh, flowering and fruiting branch (× ⅗). [After *Tyson* 5222 (MO).]

crepitans. This species has a much thicker, more fleshy fruit-wall than other species and is the only pepper in Panama which sometimes ripens with a decidedly pink hue. The distinctions between *C. frutescens* and *C. chinense* are not always clear, but most Panamanian material is identifiable by the constricted calyx and other characters mentioned above.

LOS SANTOS: Near headwaters of Río Pedregal, 25 mi. SW of Tonosí, 2,500–3,000 ft, cloud forest and native clearing, *Lewis et al. 2925* (MO).

3. **Capsicum frutescens** L., Sp. Pl. 189. 1753. LECTOTYPE: *van Royen s.n.* (L, not seen; photo in Taxon 18: 279. 1969).

Small *shrub*, herbaceous or quite woody to 2 m tall, glabrous to pubescent, mostly fine-puberulent. *Flowers*, above the first node, more than one to a node; pedicels mostly thickening and erect in fruit; calyx cyathiform to almost tubular, truncate or with small, deltoid umbos, lacking a constriction at the base near the pedicel; the corolla white or greenish, the lobes spreading to recurved; the anthers blue to violet, rarely yellow; the style exserted 1.5 mm or more beyond the anthers. Mature *fruit* erect, deciduous, soft fleshed, of various shape, mostly red.

Capsicum frutescens is a widespread species found from the southeastern United States to Argentina and has been introduced to many countries. It is slower to fruit than other species. Herbarium specimens are often indistinguishable from those of *C. annuum*.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 178* (US). CANAL ZONE: Moist thicket, Balboa, *Standley 25504* (US). Sosa Hill, Balboa, *Standley 26493* (US). PANAMÁ: Along Corozal Road near Panamá, *Standley 26862* (US). Between Matías Hernandez and Juan Díaz, *Standley 32004* (US).

5. CESTRUM

Cestrum L., Sp. Pl. 191. 1753; Gen. Pl., ed. 5. 88. 1754. *Cestrum nocturnum* L.

Parqui Adans., Fam. 2: 219. 1763. TYPE: Not designated.
Meyenia Schlecht., Linnaea 8: 251. 1833, non *Meyenia* Nees *in* Wall., Pl. As. Rar. 3: 75, 78. 1832, Acanthaceae. TYPE: *M. fasciculata* Schlecht. (= *Cestrum fasciculatum* (Schlecht.) Miers).
Lomeria Raf., Sylv. Tell. 56. 1838. TYPE: *L. purpurea* Raf. (= *Cestrum longiflorum* R. & P.).
Wadea Raf., Sylv. Tell. 56. 1838. TYPE: *W. latifolia* Raf. (= *Cestrum latifolium* Lam.).
Habrothamnus Endl., Gen. 667. 1839. TYPE: Based on *Meyenia* Schlecht.

Unarmed *shrubs* or *trees* to 12 m tall with simple or dendritic hairs, some species glabrous; trunks not exceeding 15 cm d.b.h.; twigs glabrous to velutinous, mostly slender. *Leaves* simple and entire, pinnately nerved, mostly glabrous above and variously pubescent beneath, mostly short petiolate; minor leaves present or not. *Inflorescence* axillary, sometimes appearing terminal, often bracteate, mostly a congested raceme or panicle but occasionally open or solitary and sessile; pedicels short, bracteolate. *Flowers* sometimes nocturnally opening and scented; calyx cyathiform to tubular, variously pubescent, lobed less than halfway down, the lobes sometimes unequal, not much accrescent in fruit; corolla tubular or salverform, often slightly zygomorphic, the tube obconical or with a

bulge along its length, the lobes short, often recurved, the location of pubescence often characteristic for species; stamens 5, equal or subequal, filaments inserted along the corolla tube, variously pubescent, geniculate or appendaged, the anthers clustered, included, bithecate, dehiscent longitudinally; ovary on a small glandular disc or short stipe, glabrous, 2-loculed with 4–50 ovules, the stigma included or exserted, small. *Fruit* a short-stipitate, fleshy or juicy berry, rarely with one or two apical sutures; seeds variable in shape and size; embryo straight or somewhat curved in fleshy endosperm.

A genus of 150–250 species in tropical America. Many, if not all, Old World species have been described on the basis of material introduced from the Americas. Several species are widely cultivated for ornament, but no other uses are known.

Cestrum is divisible into two sections, *Cestrum* and *Habrothamnus*. The sect. *Habrothamnus*, of which only *C. chiriquianum*, *C. aurantiacum*, and perhaps *C. jacaltenanginum* are found in Panama, differs from the typical section in its inflated-clavate corolla tube, pointed corolla lobes, many ovules, and white endosperm (yellow in sect. *Cestrum*). Section *Habrothamnus* is centered in Mexico and the Antilles and has little or no representation in South America. Section *Cestrum* may comprise species reduced or evolved from more primitive, *Habrothamnus*-like ancestors. Within section *Cestrum*, the obscurity of phylogenetic trends makes key preparation or establishment of infra-sectional groupings difficult. The last monograph (Francey, 1935–6), while thorough and correct in a classical sense, is very difficult to use. Unwieldy key format and tendency to emphasize leaf characters prevent easy association of species of like morphology, and in this treatment many species were described from insufficient range of material.

Cestrum is closely related to *Sessea* (about 30 species of the Andes), which differs in having dehiscent capsular fruits. Most species of *Sessea* have densely pubescent calyces and corollas. The distinctions between *Sessea* and *Cestrum* are not accepted by all workers, and the two genera are sometimes combined under *Cestrum* (see Francey, 1935: 49–51).

The genus was given its name because of a fancied resemblance to a plant of this name described by Dioscorides.

In Panama, twenty species are recognized. Three of these, *C. latifolium*, *C. megalophyllum*, and *C. racemosum*, are plentiful and occur frequently in neighboring countries. Many of the other species occur either as rarities or in local areas. In addition to the collections cited under the descriptions below, one collection, *Gentry 1499* (MO), must be listed as undetermined. The specimen is in fruit and was collected in August in mountains above Puerto Obaldía, Comarca de San Blas. As this region is almost unknown from a botanical standpoint, and what little is known reveals the presence of many endemic species, it is possible that this collection represents a new species.

Useful reference:

Francey, P. Monographie du genre *Cestrum* L. Candollea 6: 46–398; 7: 1–132. 1935–6.

a. Adult leaves pubescent beneath.
b. Pubescence of branched or stellate hairs.
c. Calyx more than 8 mm long; corolla tube more than 15 mm long, glabrous or pubescent outside.
d. Filaments inserted above the middle of the corolla tube; corolla tomentose outside ..... 19. *C. strigilatum*
dd. Filaments inserted below the middle of the corolla tube; corolla glabrous. ..... 5. *C. jacaltenanginum* var. *tomentosum*
cc. Calyx 3–5 mm long; corolla tube ca. 11 mm long glabrous outside .... 7. *C. lanatum*
bb. Pubescence of simple hairs or wanting.
e. Corolla tube more than 25 mm long, mostly pubescent outside; fruits white; veins mostly more than 7 on each side of the midrib, when dry elevated beneath and giving the leaf a conspicuous corrugated appearance ..... 16. *C. rugulosum*
ee. Corolla tube less than 25 mm long, glabrous outside; fruits purplish or black; veins mostly fewer than 7 on each side of the midrib, when dry not giving the leaf underside a corrugated appearance.
f. Filaments free from the corolla less than 1 mm; calyx 3 mm long; corolla tube with an abrupt, globose expansion at the apex; fruits to 15 mm long ..... 1. *C. alternifolium*
ff. Filaments free from the corolla 1.5–2.5 mm; calyx 2–2.5 mm long; corolla tube evenly obconic with little expansion at the apex; fruits to 9 mm long ..... 9. *C. latifolium*
aa. Adult leaves glabrous beneath (or a few scattered minute hairs on the principal veins).
g. Filaments with tooth-like appendages near the point of insertion.
h. Filaments manifestly dentate near the point of insertion.
i. Corolla tube less than 18 mm long; filaments free from the corolla less than 3 mm; stigma exserted.
j. Pedicels evident, 1–2 mm long, pubescent; leaves coriaceous .... 13. *C. pittieri*
jj. Pedicels wanting or very short and glabrous, leaves membranaceous ..... 12. *C. nocturnum*
ii. Corolla tube more than 18 mm long; filaments free from the corolla more than 4 mm; stigma included.
k. Corolla ca. 30 mm long; calyx 3 mm long, lobes not reflexed..... 3. *C. costaricense*
kk. Corolla ca. 26 mm long; calyx 4.5 mm long; lobes conspicuously reflexed ..... 10. *C. lewisii*
hh. Filaments tumid, gibbous, or with a rounded swelling near the point of insertion but not manifestly dentate.
l. Corolla and filaments glabrous ..... 2. *C. chiriquianum*
ll. Corolla interior or filaments at least in part pubescent.
m. Corolla tube less than 15 mm long; leaves coriaceous 11. *C. megalophyllum*
mm. Corolla more than 19 mm long; leaves membranaceous.
n. Calyx more than 8 mm long; twigs puberulent ..... 20. *C. warszewiczii*
nn. Calyx less than 6 mm long; twigs glabrous ..... 4. *C. gracile*
gg. Filaments unappendaged (sometimes pubescent or barbellate).
o. Calyx more than 7 mm long ..... 20. *C. warszewiczii*
oo. Calyx less than 6 mm long.
p. Corolla tube less than 15 mm long.
q. Filaments mostly more than 3 mm free from the corolla; leaves mostly acute to deltoid in the lower third, often very large, in Panama mostly drying black ..... 11. *C. megalophyllum*
qq. Filaments mostly free from the corolla less than 3 mm; leaves mostly rounded or obtuse in the lower portion, seldom drying black.
r. Veins mostly more than 10 on each side of the midvein, evenly spaced and parallel ..... 14. *C. racemosum*
rr. Veins mostly fewer than 10 on each side of the midvein, well or ill spaced.
s. Venation obscure above, nearly at right angles to the midvein; leaves drying dark above; inflorescences borne on slender twigs ..... 18. *C. standleyi*

ss. Venation prominent, at ca. 45° to the midvein; leaves drying light green, often greyish or yellowish; inflorescences borne on stout mature wood ..... 6. *johnniegentrianum*

pp. Corolla tube more than 17 mm long.

t. Inflorescence an open, slender, pendant panicle, terminal or on elongate axillary shoots; filaments free from the corolla less than 2.5 mm.

u. Twigs and inflorescence whitish puberulent; pedicels wanting; plants usually drying with a brownish or greyish cast ..... 15. *C. reflexum*

uu. Twigs and inflorescences glabrous (rarely glabrate); flowers with short but distinct pedicels (note bracteole position); plants usually drying greenish or yellowish ..... 17. *C. scandens*

tt. Inflorescence a congested terminal or axillary panicle of clustered short racemes or panicles; filaments free from the corolla 3 mm or more.

v. Filaments free from the corolla ca. 3 mm; corolla tube more than 22 mm long ..... 8. *C. langeanum*

vv. Filaments free from the corolla more than 4 mm; corolla tube less than 20 mm long.

w. Pedicels ca. 1 mm long; calyx 3–4 mm long; plants drying dark brown ..... 4. *C. gracile*

ww. Pedicels 3.5–6 mm long; calyx ca. 5 mm long; plants mostly drying bright green ..... 2. *C. chiriquianum*

1. **Cestrum alternifolium** (Jacq.) O. E. Schulz *in* Urb., Symb. Antill. 6: 270. 1909–10; 7: 555. 1911.

Ixora alternifolia Jacq., Enum. Pl. Carib. 12. 1760; Sel. Stirp. Amer. 16, *tab. 177*. 1763.
TYPE: Herb. Jacquin (W, not seen; MO, photo).

Cestrum alternifolium var. *mitanthum* O. E. Schulz *in* Urb., Symb. Antill. 6: 273. 1909–10.
TYPE: Colombia (Isla Margarita), *Johnston 285* (MO).

Shrub or *tree* to 6 m tall; twigs glabrous to puberulent, sometimes tomentose. *Leaves* small, mostly to ca. 5 cm long, elliptical, mostly acute or obtuse apically and basally, glabrous or puberulent above, beneath puberulent on the veins and vestite with scattered or dense hairs on the lamina; petiole to 5 mm long; minor leaves large or absent. *Inflorescence* axillary or terminal, several flowers congested on a short, stout peduncle; pedicels short, glabrous, becoming stout in fruit. *Flowers* inconspicuous, calyx to 3 mm long, glabrous within and pilose outside, the nerves obscure; corolla greenish-yellow, the tube ca. 20 mm long, slender with a bulbous enlargement at the apex, glabrous outside, sparingly pubescent within, sometimes pilose at the base, the lobes lanceolate, 4–6 mm long; stamens equal, the filaments inserted at the apex of the corolla tube, 0.5 mm long free, straight, edentate, smooth, glabrous, the anthers oblong, 0.75 mm long; ovary stipitate, the ovules ca. 10, the stigma included but exceeding the anthers by 1 mm. *Fruit* to 15 mm long, obovoid, ripening through pink to purple-black; seeds 5.5 mm long.

The small pubescent leaves and the bulb at the top of the corolla tube distinguish this species from other species of *Cestrum* growing in Panama. Fruiting specimens may be difficult to separate from small-leaved specimens of *C. latifolium*.

Cestrum alternifolium occurs from Venezuela to Mexico and in the Antilles, but in Panama, to judge from the number of collections, it is not a common plant. All Panamanian collections seen have been from lowlands near the Pacific, either on the south coast of the Isthmus or on offshore islands.

CANAL ZONE: Fort Amador on causeway and islands, *Tyson 2025* (FSU). CHIRIQUÍ: Roadside 4 mi. E of Concepción, *D'Arcy 5302* (MO). Near San Felix, 0–120 m, *Pittier 5440* (NY, US). PANAMÁ: Near beach at Nueva Gorgona, *Duke 4510* (GH, MO.). Bella Vista, *Heriberto 227* (US). La Exposición, *Heriberto 243* (US). Taboga Island, more or less forested slopes, *Macbride 2767* (F, GH, US). Taboga Island, *Miller 1839* (US). Taboguilla Island, *Miller 1984* (US). Bella Vista, brushy field, *Standley 25399* (F, MO, US). Taboga Island, moist thicket, *Standley 27020* (MO, US). Taboga Island, brushy slope, *Standley 27842* (GH, US). VERAGUAS: Río San Francisco, *Dwyer 1271* (MO).

2. **Cestrum chiriquianum** Francey, Candollea 6: 96–97. 1936. LECTOTYPE: Chiriquí, *Pittier 3210* (F-600250; US, isolectotype).

Slender *shrub* 3 m tall; twigs green, soon turning to straw color. *Leaves* 7–12 cm long, elliptical, obtuse or acuminate apically and basally, margins slightly revolute, glabrous, the lateral venation obscure; petioles 1–1.5 cm long, narrowly winged; minor leaves wanting. *Inflorescence* a few flowered, terminal panicle; peduncle slender, 4–5 cm long; pedicels ca. 1 mm long, glabrous. *Flowers* showy, blue-violet, calyx 3–4 mm long, glabrous and drying dark, the lobes 1 mm long, short deltoid and cuculate, prominently costate; corolla tube 17–19 mm long, glabrous, slender at the base and broadening in the upper half to 5 mm across at the apex, the lobes deltoid, ca. 3 mm long; stamens equal, the filaments adnate to slightly above the middle of the tube, ca. 5 mm free, glabrous, tumid and prominently geniculate at the point of insertion, anthers rotund, 1 mm across, golden brown; ovary on a glandular stipe, ovules ca. 10, the stigma exserted 2 mm beyond the included anthers. *Fruit* unknown.

This species has a corolla like those in sect. *Habrothamnus*, but the calyx is small and resembles those in sect. *Cestrum*. The purplish, broad-mouthed corolla shape and small calyx together with the absence of pubescence will distinguish this from other Panamanian species of *Cestrum*. It occurs in Panama and in Costa Rica (*Davidse et al. 1617* (DUKE, F, MO, NSW)).

CHIRIQUÍ: Above Boquete, in forest 1,650–1,800 m, *Dressler & Williams 4002* (MO). Between the Río Ladrillo and Los Siguas Camp, southern slope of Cerro de la Horqueta, 1,200–1,700 m, *Maxon 5411* (F, US). Humid forest around Los Siguas Camp, southern slope of Cerro de la Horqueta, 1,700 m, *Maxon 5436* (US). Humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2,100–2,263 m, *Pittier 3210* (F, US). Southern slopes of Cerro Horqueta, N of Boquete, 6,500 ft, *Wilbur et al. 13477* (DUKE). Above San Ramón near Bajo Mono, Boquete District, 6,000 ft, *Wilbur et al. 13540* (DUKE).

3. **Cestrum costaricense** Francey, Candollea 6: 368. 1935. SYNTYPES: Barba, Costa Rica, *Brade 2306* (not seen); Veraguas, *Warszewicz 4* (not seen).[7]

Branches slender, flexuous, terete, 1–3 mm in diameter, finely striate, smooth, trigonous and angular above, pale brown or brownish-red. *Leaves* medium-sized, 57–96 mm long and 23–29 mm broad, erect-spreading, ovate or elliptic-lanceolate, acute or rounded at the base, not decurrent, acuminate at the apex, subcoriaceous, rigid, the margin minutely revolute, undulate, above brown or yellow-green or brownish green, dull, often rugose and minutely pulverulent-granulate, manifestly paler, dull green and glabrous below, the midvein slender, dark brown

[7] The type material of this species was destroyed at Berlin, and no duplicates have been located. As no material of this species was available for study, a translation of Francey's original description is presented here.

and inconspicuous above, prominent brown beneath, lateral veins 5–7 on each side, ascending-arcuate, more or less impressed and smooth or reticulate impressed above, beneath reticulate-nerved and prominent; petiole manifest, articulating at the nodes, contorted, stout, flexuous, 8–12 mm long and 0.7–1.2 mm thick, terete, channeled above, glabrous, the base often hook-like; minor leaves wanting. *Panicles* terminal, 60–95 mm long, many flowered, the axes 35–55 mm long and 0.6–1 mm thick, trigonous, angular, striate, glabrate, brown or dark purplish; peduncles wanting above, below 6–30 mm long and 0.5 mm thick, 8–10-flowered, glabrous; pedicels 2–3 mm long and 0.5 mm thick, terete, glabrous; bracts 5–10 mm long, 0.5–1 mm wide, linear lanceolate, very long acuminate, glabrous. *Flowers* violet, crowded; calyx 4.5 mm long and 2 mm across, campanulate, angular, subcoriaceous, glabrous inside and out, 5-dentate, 5-nerved, teeth slightly reflexed, 1 mm long and 1 mm broad, triangular, acuminate, subcuspidate, the margin glabrous, the nerves thick, somewhat raised, lateral nerves almost wanting; corolla 26 mm long, the tube 20.5 mm long, contracted below the ovary then subcylindrical, hardly obconical, inflated at the apex, constricted below the limb, glabrous inside and out, the lobes 5.5 mm long and 2 mm wide, ovate-lanceolate, acuminate, glabrous inside and out, puberulent at the margin; stamens 20 mm long, equal filaments adnate for ¾ the length of the tube (14 mm), 6 mm free, dentate and hirsute 1 mm below the point of insertion then straight, glabrous, the adnate portion hirsute, the teeth (appendages) 1 mm long, anthers cordate, 1 mm long; ovary oblong-globose, 1 mm long and 0.7 mm across, glabrous, 12-ovuled, the stipe obconic, the style 21 mm long, glabrous but puberulent at the apex, filiform, surpassing the stamens 1 mm, stigma capitate, puberulent, included. *Fruit* unknown.

"The calyx is the most striking organ of this species with its teeth slightly bent outwards" (Francey).

From the above description it is difficult to suggest affinities of this species. The color, pubescence, and shape of the corolla and the pubescence and teeth of the filaments are suggestive of *C. dumetorum* Schlecht. of Mexico and Central America and of *C. poasanum* Donn. Sm. of Costa Rica.

Known only from the two syntype collections noted above and now destroyed.

VERAGUAS: *Warszewicz 4* (not seen).

4. **Cestrum gracile** Francey, Candollea 6: 366. 1935. TYPE: Veraguas, *Warszewicz 3* (not seen).[8]

Branches flexuous, below terete and defoliate, above foliaceous and floriferous, 1–2.5 mm thick, angular, striate, minutely costate, glabrous, dull brown or brownish grey. *Leaves* small, 42–55 mm long, 12–17 mm broad, manifestly petiolate, spreading or erect, often plicate, ovate-lanceolate, the base acute and decurrent into the petiole, the apex attenuate, acuminate, the margin revolute, glabrous on both sides, coriaceous, brown or dark brown, shining above, dull and paler below, the midvein slightly impressed or inconspicuous above, con-

[8] The type specimen of this species was destroyed at Berlin (B), and the duplicate was not located at Geneva (G). As no material of this species was available for study, a translation of Francey's original description is presented here:

spicuous beneath, the 6, regular, lateral nerves ascending on each side conspicuous above and beneath; petioles 7–10 mm long, blackening, the base slightly thickened, 0.5–0.7 mm thick, terete beneath, sulcate above, glabrous; minor leaves absent. *Corymbs* elongate, located in the axils of the terminal leaves, sparsely foliaceous, 10–15-flowered, 40–70 mm long; axes and peduncles filiform, 0.3–0.5 mm thick, striate-channeled, glabrous, brown; floral leaves like those of the branches but smaller, 8–27 mm long, 2.5–8 mm broad; peduncles one-flowered, 6 mm long, 0.3 mm in diameter, thickened at the apex, glabrous; pedicels 3.5–6 mm long, 0.5 mm in diameter, terete, channeled, glabrous. *Flowers* 23.5 mm long, calyx attenuate into the pedicel, obconic-tubulose, 5 mm long, 1.7 mm in diameter, terete, barely costate, glabrous inside and out, 5-dentate, 5-nerved, the teeth unequal, 0.7–1 mm long and 1 mm wide, the margin darkened, glabrous, the nerves hardly raised, lateral nerves wanting; corolla stalked (1 mm), 21.5 mm long, the tube 17 mm long, contracted below the ovary then infundibuliform, hardly expanded at the apex, constricted below the limb, glabrous inside and out, the lobes of the limb 4.5 mm long, introflexed, triangular-lanceolate, basally 2 mm wide, acuminate, 3 mm wide when expanded, ovate lanceolate, very acute, glabrous and glandular outside, glabrous inside, the margin densely short pilose outside; stamens 16 mm long, subequal, the filaments adnate for ⅔ the length of the tube (7–7.5 mm), 8.5–9 mm free, the base of the free part slightly thickened and elevated but edentate and not geniculate, glabrous overall, the anthers rotund, 1 mm broad; ovary ovoid, 1.2 mm long and 1 mm across, glabrous, 11-ovuled, the disc glandular, the style 17.5 mm long, filiform, hardly thickened at the apex, hardly puberulent, exceeding the stamens by 1.5 mm, the stigma capitate, puberulent, included. *Berry* unknown.

"As indicated by the numerous characters indicated in the analytical key [Francey's], *C. gracile* is rather difficult to distinguish from *C. anagyris* in a systematic way. However, the separation is always easy at a glance for the first named is of a dark brown color, while the second is much lighter, generally of a bright green" (Francey).

Francey's key separates *C. gracile* from *C. anagyris* by the smaller leaves, obscurity of lateral veins on the leaf undersides, the calyx conical-tubular and gradually attenuate into the pedicel rather than tubular and abruptly contracted to the pedicel, and the more slender corolla tube. *C. anagyris* Dun. in DC. (Prodr. 13(1): 608. 1852) occurs in central Mexico.

Known only from the type collection.

VERAGUAS: *Warszewicz 3* (not seen).

5. **Cestrum jacaltenanginum** var. **tomentosum** Francey, Candollea 6: 119. 1935. TYPE: Veraguas, *Warszewicz 1* (not seen).[9]

Leaves densely stellate-tomentose. *Flowers* with the calyx 10 mm long, lobes 3–4 mm long and 1 mm wide; corolla tube regular, obconic-infundibuliform,

[9] The type collection of this variety was destroyed at Berlin (B), and no duplicates have been located. As no material of this species was available for study, a translation of Francey's original description is presented here.

strongly constricted under the limb, the lobes 2 mm long and 2 mm wide, triangular, obtuse and very shortly mucronate; filaments inserted at ⅓ the length of the tube, 12 mm long, free, the base slightly thickened, straight, edentate, glabrous.

Francey separates this variety from var. *jacaltenanginum* by its longer calyx and longer lobes. *Cestrum jacaltenanginum* Loesener (Verh. Bot. Ver. Prov. Brand. 65: 98. 1923) is based on a collection of *Seler* (*2641*, B) from Guatemala. A photo of this type at the Smithsonian Institution is annotated as *Cestrum regelii* Planch. by C. V. Morton (1936).

Without recourse to the original collection or discovery of other Panamanian material, it is purposeless to speculate on the affinities or placement of this variety. No other specimens of *Cestrum* from sect. *Habrothamnus* with stellate tomentum have been reported or seen from Panama.

Known only from the type collection.

VERAGUAS: *Warszewicz 1* (not seen).

6. **Cestrum johnniegentrianum** D'Arcy.[10] HOLOTYPE: Panama, *Lewis et al. 1717* (MO).

Weak *shrub* to 2 m tall, glabrate, the pubescent emergent parts glabrescent long before attaining full size; twigs drying black, soon becoming stout, slightly furrowed, drying light grey to straw colored when mature. *Leaves* ovate or broadly elliptical, ca. 15 cm long and 8 cm broad, apically acute or obtuse, basally obtuse, coriaceous, drying light green, sometimes greyish or yellowish green, the surface dull with an unusual, punctate texture when viewed under magnification; the veins prominent, 6–10 on each side of the midvein, the lamina upfolded from the midrib; petioles stout, 15–20 mm long, narrowly channelled above, drying dark; minor leaves wanting. *Inflorescences* several short, several flowered racemes in the axils of leaves on mature wood; the peduncle 4–6 mm long, mostly slender, angled, loosely and sparingly pubescent with pulverulent or distorted trichomes; pedicels wanting, bracteoles ca. 2 mm long, pubescent, sometimes equalling the calyx. *Flowers* small, calyx glabrous, short-tubular 1–2 mm long, slightly angled but otherwise ecostate, the lobes unequal, deltoid, 0.3 mm long; corolla white, 13 mm long overall, the tube ca. 10 mm long, slender, cylindrical, expanding around the anthers and contracting somewhat above them glabrous inside and out, the lobes narrowly deltoid, ca. 1 mm long, glabrate; stamens subequal, filaments straight, smooth, glabrous, 1 mm free, the anthers located ca. 1 mm short of the mouth of the corolla tube, as long as broad, ca. 0.5 mm long; stigma green, included but slightly exceeding the anthers. *Fruit* magenta, obovoid, ca. 4 mm long (?immature), the calyx not accrescent.

With its large coriaceous leaves, this species is superficially similar to *C. megalophyllum*, but the glabrous flowers are much smaller and the texture of

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[10] *Cestrum johnniegentrianum* D'Arcy, sp. nov. Frutex usque ad 2 m; foliis glabris coriaceis, late ovatis; floribus subsessilibus; filamentis ad tubo corollae ¾ longitudinis adnatis, ca. 1 mm discretis.

Nomen Johannis L. Gentryi, deicipuli Solanacearum Guatemalensium, designatur ad hoc specie.

the leaves under magnification is very different. The lower portion of the leaves is broader than in most *C. megalophyllum*. Also resembling *C. pittieri*, this species lacks appendages on the filaments of the stamens.

COCLÉ: Mountains N of El Valle de Antón, 2,500–3,000 ft, *Lewis et al. 1717, 1734* (both MO). Along road and in wet forest 5 mi. NW of El Valle de Antón, 1,000 m, *Luteyn 1226* (MO).

7. **Cestrum lanatum** Mart. & Gal., Bull. Acad. Roy. Sci. 12: 146. 1842. TYPE: Mexico, *Galeotti 1208* (NY, US).

C. densiflorum Francey, Candollea 6: 195. 1936. SYNTYPES: Venezuela, *Pittier 13294* (F, NY, MO), *13323* (NY, MO).
C. densiflorum var. *puberulum* Francey, Candollea 6: 196. 1936. TYPE: Venezuela, *Pittier 13323* (F).

Tree to 12 m tall; twigs loosely tomentose with dendritic hairs, soon glabrescent. *Leaves* to 10 cm long, elliptical, obtuse, acute at each end, above with dendritic hairs in the basal portion when emerging, glabrate and drying dark when mature, beneath with a loose caducous tomentum; petioles to 3 cm long but mostly much shorter; minor leaves wanting or very small. *Inflorescences* several, mostly short racemes or panicles, axillary and terminal, several flowered; peduncles slender, tomentose or glabrescent, mostly ebracteate; pedicels and bracteoles obsolete. *Flowers* drying dark grayish, the calyx 3–5 mm long, campanulate, densely tomentose outside with 5 short, unequal lobes, glabrescent and broadening but not lengthening in fruit; corolla greenish, the tube short, ca. 11 mm long, glabrous outside, sparingly pubescent along the filament adnation inside, the lobes ca. 4 mm long; stamens equal, the filaments 3.5–4.5 mm free, geniculate, barbellate and gibbous but not truly dentate at the point of insertion; ovary with about 8 ovules, the stigma included. *Berry* (Francey) ellipsoid, 7 mm long.

This species and *C. jacaltenanginum* var. *tomentosum* are the only taxa of *Cestrum* occurring in Chiriquí which have a tomentum of dendritic hairs. *Cestrum lanatum* has the straight-sided, tubular flowers of sect. *Cestrum*, while var. *tomentosum* has the obconical, apically saccate flowers of sect. *Habrothamnus*. *Cestrum strigilatum* of lowland eastern Panama also has dentritic hairs.

While similar to material in various herbaria annotated by Francey as *Cestrum hirsutum* Jacq. (Hort. Schoenbrum. 3: 41, *tab. 324.* 1798. Type W, not seen), the leaves are of a very different texture, appearing quite thick and sometimes almost felty, while those of *C. hirsutum* are very thin, almost membranaceous. Leaves of *C. lanatum* often have a bluish or brownish cast, while those of *C. hirsutum* dry bright green.

This species ranges from Venezuela through Panama west to Mexico. In Panama it is known only from middle and upper elevations in Chiriquí Province.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1,500–2,000 m, *Allen 1484* (GH, MO, US). Bajo Mono, Boquete District, 4,500 ft, *Davidson 463* (A, F, MO), *465* (MO). 6 m NE of El Volcán, 7,400–7,500 ft, deep moist canyon bottom, *Tyson 822, 823* (FSU, MO). West slope of El Baru between 7,000–8,000 ft, *Tyson & Loftin 5988* (MO). Upper Río Chiriquí Viejo, *White 341* (MO, US). Lava field and slopes between Volcán de Chiriquí and Cerro Aguacate, 6,500–7,200 ft, *Wilbur & Teeri 13330* (DUKE).

8. **Cestrum langeanum** D'Arcy.[11] HOLOTYPE: Panama, *Dressler & Williams 3965* (MO).

Shrub 3 m tall, twigs pulverulent-tomentose with a soon-deciduous indument of sparingly branched, multicellular, distorted trichomes, young branches slender, uniformly finely striate and perhaps purplish at the nodes. *Leaves* mostly 15 cm long and 5 cm wide, ovate, lanceolate or elongate, apically acute or slightly acuminate, basally obtuse, chartaceous and glabrous, the upper surface shiny, beneath dull with 8–10 contrasting veins on each side of the midvein; petioles short, ca. 10 mm long, moderately stout; minor leaves wanting. *Inflorescence* a terminal, congested, many-flowered panicle comprising a series of panicles axillary to the terminal leaves, the ultimate leaf (bract) reduced to 5 cm long and 2 cm broad; peduncles 1.5–3 cm long, pubescent, flattened, and grooved; pedicels very short or wanting, the bracteoles narrowly lanceolate or oblong, 4–5 mm long, pubescent or not. *Flowers* with the calyx 3 mm long, short-tubular, angled to the costae of the lobes, pubescent outside with a shiny, glandular appearance, inside glabrous with prominent venation, the lobes 1 mm long, equal, obtuse, slightly cucullate; corolla green, 30 mm long overall, the tube ca. 25 mm long, slender, expanding around the anthers and contracting somewhat above them, glabrous inside and out, the lobes 5–6 mm long, oblong, minutely puberulent inside and out; stamens equal, the filaments glabrous, smooth, straight, adnate ca. 18 mm up the corolla tube, 3 mm free, anthers orange, broader than long, ca. 0.75 mm long, situated well within the corolla tube ca. 2 mm short of its mouth; ovary obtuse-conical, the upper ⅓ consisting of sterile, nectariferous (?) tissue, ovules ca. 4, the included stigma situated 0.2–1.0 mm above the anthers, abruptly obconical with a discoid apex. *Fruit* unknown.

Vegetatively this species resembles *C. megalophyllum* Dun., but the terminal inflorescence and longer flowers are ready points of distinction. The glabrous filaments and occurrence of branched hairs on twigs and peduncles are also diagnostic. The position of the anthers is relatively lower in the tube than most other species of *Cestrum*.

This species is known only from the type collection, taken from lowland cloud forest near the Caribbean coast of central Panama.

This species is dedicated to Carla Lange, Missouri Botanical Garden, whose bibliographic assistance has eased the tasks of many botanists.

COLÓN: Santa Rita lumber road ca. 15 km E of Colón, *Dressler & Williams 3965* (MO).

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[11] *Cestrum langeanum* D'Arcy, sp. nov. Frutex 3 m altus, ramunculis pulverulento-tomentosis mox glabris trichomatibus parce ramosis pluricellularibus imperfectis; inflorescentia terminalis multiflorida pluribus paniculis conferta axillaribus constans, pedunculis 1.5–3 cm longis pubescentibus complanatis sulcatis, pedicellis carentibus, bracteolis lanceolatis, 4–5 mm longis, pubescentibus vel. glabris; calyx 3 mm longus, tubulosus, extus pubescens, nitidus, glandulosus, intus venis prominentibus, lobis 1 mm longis, aequalibus, obtusis, cucullatis, corolla viridi, 30 mm longa, tubo 25 mm longo, gracilis, utrinque glabro, lobis 5–6 mm longis, oblongis, puberulentibus utrinque; staminibus aequalibus, filamentiis glabris, laevis, rectis, 3 mm libris; ovulibus circa 4; acini haud suppetunt.

9. **Cestrum latifolium** Lam., Illustr. 2: 5. 1793. TYPE: Herb. Lamarck (P-Lam).

C. tenuiflorum Kunth *in* H. & B., Nov. Gen. 3: 61. 1818. TYPE: Oronoco, *Bonpland 1017* (P; IDC 6209. 63: II. 3).
C. chloranthum Dun. *in* DC., Prodr. 13(1): 636. 1852. TYPE: Trinidad, *Sieber 143* (G-DC, MO).
C. bilbergianum Beurl., Kongl. Vetensk. Acad. Handl. 1854: 140. 1854. TYPE: Portobelo, Panama, *Bilberg s.n.* (not seen, placed in synonomy here by Francey (1935: 291).
C. albopunctatum Dun. *in* DC., Prodr. 13(1): 635. 1852. TYPE: Peru, *Poeppig 2979*, (G-DC, not seen; US, photo).
C. latifolium var. *tenuiflorum* (Kunth) O. E. Schulz *in* Urb., Symb. Antill. 6: 270. 1909–10.

Shrub or *tree* to 12 m tall; twigs glabrous or puberulent, soon becoming greenish yellow. *Leaves* to 25 cm long, ovate or elliptic, often oblique, apically acute or acuminate, basally rounded or obtuse with scattered, short, simple hairs on both sides, more frequent on the lower surface especially along the conspicuous major veins; petioles to 4 cm long, puberulent; minor leaves wanting. *Inflorescences* many, short racemes or short-branched panicles, axillary or terminal; peduncles to 1.5 cm long, pubescent, many-flowered; pedicels to 1 mm long with short bracteoles. Flowers caducous, the calyx 1–2 mm long, campanulate, yellowish, puberulent outside, glabrous within, with 5 short-dentate lobes; corolla whitish-yellow, sometimes with purple blotches, the tube to 20 mm long, slender but gradually widening at the apex, glabrous outside, inside pubescent at the base and often above the middle as well, lobes ca. 2 mm long, narrowly deltoid; stamens equal, the filaments 1–3 mm free, barbellate to densely pilose about 3 mm below the anthers (at or just below the point of insertion); ovary with about 8 ovules, the stigma included. *Fruit* a juicy berry, 5–9 mm long, obovate, ripening through pink to shiny black; seeds several.

This is a common weedy tree in lowland Panama ranging east to the Guianas and Brazil and west to Nicaragua. It is present in the Antilles. When in full bloom the tree is showy, but flowers are easily dislodged and few herbarium specimens retain more than a small representation of the blooms on the twig.

Cestrum latifolium is easily recognized by its pubescent leaves, which are usually broad and oblique. Small-leaved specimens in fruit may be difficult to distinguish from those of *C. alternifolium.* In the field, this species is identifiable by its arboreal stature and weedy occurrence in fence rows, pastures and other sites of recent disturbance. It flowers sporadically, most branches then heavily laden with flowers for a short time.

CANAL ZONE: Near Juan Mina, *Bartlett & Lasser 16568* (MO). End of side road off Chiva-Chiva road ca. 1 mi from Gaillard road, *Blum 466* (FSU, MO, PMA). Vicinity Tropic Test Center Albrook Tower, *Blum 570* (FSU, MO). Colón to Empire, Panama Railroad, *Crawford 446* (NY). Road C2C on Cerro Luisa, *Croat 10777* (MO). Rear lighthouse clearing, Barro Colorado Island, *Croat 11996* (MO). Cerro Luisa near Pedro Miguel, *Croat 12381* (MO). Roadside between Madden Wye and Summit Naval Radio Station, *Croat 15012* (G, MO, NY, W). Chagres River near Gamboa railroad bridge, *Croat 15243* (MO). Lighthouse clearing no. 2, B.C.I., *D'Arcy 4295* (MO). Ft. Kobbe, *Duke 3927* (GH, MO). Near beach at Ft. Kobbe, *Duke 4243* (MO), 4692 (GH, MO, US). Near the sea beneath Thatcher Bridge, south side of Canal, *D'Arcy & D'Arcy 6080* (ADW, BIRM, C, CAL, COI, COL, CORD, DAO, DUKE, F, FSU, G, GH, K, L, LE, M, MO, MPU, NY, P, PMA, POM, PRE, R, TH, UCWI, US, VEN, WIS). Carretera de Gamboa, *Duran 40* (MO). Gatun near locks, *Dwyer 1777* (MO). U. S. Army Tropic Test Center, Albrook, *Dwyer 6713* (DUKE, MO). Madden Dam, Boy Scout Camp Road, roadside woods, *Dwyer & Elias 7474* (GH, MO, US). Madden

Dam, second growth, *Ebinger 841* (GH, MO, US). Madden Forest, *Florez 41* (MO). Curundu near Air Force Survival School, *Gentry 1592* (MO). Near Madden Dam, *Kant 11* (MO). Boy Scout Camp Road off Madden Dam Road, *Kirkbride 44* (MO, NY). Gamboa, open grassy *Cecropia-Erythrina* second growth near riding stables, *McDaniel 5043* (MO). Curundu, Thunder Hill, *McDaniel 5187* (FSU, MO). Vicinity of Madden Dam, near Río Chagres, 50–75 m, *Seibert 557* (GH, MO, NY). Albrook Research Forest Site near Albrook Air Force Base, *Stimson et al. 5058* (DUKE, GH), *5080* (DUKE, FSU, NY), *5142* (DUKE, MO, NY). Curundu, Survival School area, *Tyson 1307* (MO, PMA), *1319* (FSU, MO). 4–6 mi. N of Gamboa on pipeline road, *Tyson 1484* (MO). Miraflores N of island, *White 119* (F, GH, MO). Vicinity of Miraflores Lake, *White 258* (GH, MO, US). CHIRIQUÍ: Río Macho de Monte, 1 mi. E of Cuesta de Piedra, 2,800 ft, *Tyson 895* (MO). COLÓN: Camino a San Lorenzo despues de Fort Sherman, *Quistgaard 5* (DUKE, MO). DARIÉN: Swampy disturbed forest near airport, El Real, *Croat & Porter 15461* (MO). Along Río Pirre near Río Tuira, *D'Arcy 5517* (ADW, BIRM, F, G, MO, MPU). Road from El Real to Pinogana, *Duke 4892* (GH, MO, US). 3 mi. N of Santa Fé, *Tyson et al. 4618* (FSU, GH, MO, OS, US). Vicinity of El Real, edge of road on Don Pablo Othon's farm, *Stern et al. 807* (GH, MO, US). LOS SANTOS: Los Toretos, *Dwyer 2415* (FSU), 2452 (FSU, MO), *2896* (MO). PANAMÁ: Vicinity of Río Pescado at SE part of Gatun Lake, *Bartlett & Lasser 16594* (MO). Woods along Pan American Highway halfway between El Llano and Río Mamoní, *Duke 5532* (MO). Road between Bodega Bay and Río Mata Puerco, *Duke 12514* (OS). Tocumen, *Dwyer & Hayden 15* (MO). Tocumen near airport, *Dwyer 1078* (MO). Goofy Lake to 8 mi. S of Goofy Lake toward Cerro Jefe, *Dwyer 7120* (MO, US). Open scrub, northern end of San José Island, *Erlanson 404* (G, NA, US). Near Chilibre, *Gonzalez 43* (MO). San José Island, valley one mi. E of camp, *Johnston 439* (GH, MO). Camino hacia el Río La Puente, Calzada Larga, *Quistgaard 48* (MO). Sabanas, *Riley 115* (BM, MO, US). Nuevo Emperado cerca de Arraijan, *Rosario 54* (DUKE, MO). Vicinity of Juan Franco Race Track, near Panamá, moist thicket, *Standley 27760* (GH, MO, US). San José Island, secondary growth in old military road leading inland from Ensenada La Bodega, *Stimson 5314* (DUKE, MO, NY). 5 mi. E of Cañita and 23 mi. E of Chepo, *Tyson & Smith 4162* (FSU, MO). SAN BLAS: Ailigandi, *Dwyer 6822A* (MO). VERAGUAS: Just W of Santiago, weedy roadside, *D'Arcy 5275* (ADW, C, G, GH, MO, NY, P, W). Río San Francisco, *Dwyer 1271* (MO). Vicinity of Ponuga, roadside thicket, *Dwyer & Kirkbride 7442* (BIRM, C, MO, UCWI). Between Tolé and Santiago, 50 mi. from Santiago down embankment to river edge, *Kirkbride & Hayden 168* (MO, NY). Vicinity of Santiago in cultivated land, *Stern et al. 995* (GH, MO, US). 5 mi. E of Santiago, *Tyson et al. 4288* (MO).

10. **Cestrum lewisii** D'Arcy, Phytologia 25: 116. 1973. TYPE: Based on *C. acuminatum* Francey.

C. acuminatum Francey, Candollea 6: 348, 1935, non *C. acuminatum* Sweet, Hort. Brit., ed. 2: 388. 1830. TYPE: Costa Rica, *Standley & Valerio 52237* (F).

Glabrous *shrub* or small *tree* to 7 m tall; twigs stout or slender, drying stramineous. *Leaves* mostly 10–15 cm long, narrowly ovate or elliptical, narrowed at each end, the apex long acuminate, the margins slightly revolute, 6–10 inconspicuous veins on each side of the midvein, drying yellowish green; petioles slender, ca. 1 cm long; minor leaves present or not. *Inflorescences* several, axillary or terminal; the peduncle 3–8 cm long bearing several leafy bracts and resembling a slightly reduced leafy shoot, the flowers terminal on the axis in a small, several-flowered panicle; pedicels short or obsolete, rarely to 3 mm long, leaving a cicatrix on the peduncle; bracteoles conspicuous, 3–4(–10) mm long, lanceolate. *Flowers* slender, calyx 4–5 mm long, campanulate or short tubular, glabrous, prominently costate with prominent, sometimes reflexed acuminate lobes; corolla greenish, sometimes tinged with purple, the tube 24–30 mm long, slender but widening in the upper portion to ca. 3.5 mm across, outside glabrous, inside sparingly pubescent below the point of stamen insertion, the lobes 5–7 mm

long, lanceolate; stamens equal, filaments 5 mm free, geniculate, tumid, dentate and sometimes barbellate at the point of insertion, puberulent below. *Fruit* dark, ca. 8 mm long, obovoid.

This species is distinguished by the small panicles situated at the end of leafy shoots, the absence of pubescence except within the corolla, and the barbellate and dentate filaments. The leaves resemble those of *C. chiriquianum* Francey, but the flowers are much longer. The calyx shape is suggestive of sect. *Habrothamnus*, but the corolla, while it does broaden somewhat in the upper portion, is a shape common in sect. *Cestrum*.

Cestrum lewisii is known only from the type collection and the Panamanian collections listed here.

CHIRIQUÍ: Bajo Chorro, Boquete District, 6,000 ft, *Davidson 420* (F). Bajo Chorro, Boquete District, 7,000 ft, *Davidson 433* (A, F, MO). Forested slopes above San Ramon, 4 mi. NW of Boquete, 6,000 ft, *Wilbur et al. 13535* (MO). Mossy forest along Río Chiriquí Viejo ca. 2 mi. NE of Cerro Punta, ridge of Cerro Respinga, 7,000 ft, *Wilbur et al. 13095* (MO).

11. **Cestrum megalophyllum** Dun. *in* DC., Prodr., 13(1): 638. 1852. TYPE: Trinidad, *Sieber 176* (G-DC, MO).

C. claussenii Dun. *in DC. Prodr.* 13(1): 637. 1852. TYPE: Brazil, *Claussen s.n.* (MPU).
C. baenitzii Lingelsh., Fedde Repert 7: 248. 1909. TYPE: Bolivia, *Bang 1634* (MO).
C. sylvaticum Francey, Candollea 6: 316–7. 1935. TYPE: Peru, *Killip & Smith 25483* (F, US).

Shrub or *tree* to 8 m tall; twigs stout, puberulent with short, simple hairs, soon glabrescent and striate-barked. *Leaves* large, to 30 cm long, elliptic or obovate, broadest above the middle, apically acute or acuminate, basally acute or rounded, the margins often revolute, coriaceous, glabrous at maturity or with a few scattered hairs on the midvein beneath, the veins prominent beneath, lateral veins 5–10 on each side, often drying dark; petioles to 2.5 cm long, stout, glabrous; minor leaves mostly wanting. *Inflorescences* congested axillary fascicles or short racemes, numerous along the branches; the peduncles to 1.5 cm long, mostly unbranched, puberulent; pedicels short or wanting, bracteoles ca. 0.5 mm long, puberulent. *Flowers* inconspicuous, the calyx 2–4 mm long, short-tubular, puberulent or glabrous outside, glabrous within, the lobes short, often unequal, costate; corolla greenish white, the tube 10–15 mm long, slender, enlarging in the upper portion, glabrous outside, mostly tomentose at the base within, the lobes 3 mm long, lanceolate; stamens equal, the filaments 3–3.5 mm free, pubescent near the point of insertion and at the base, straight, mostly not geniculate, tumid or appendaged at the point of insertion but occasionally short gibbous; stigma included but exceeding the anthers by 1 mm. *Fruit* elliptical or obovoid, ca. 8 mm long, maturing black.

The flowers of this species are seldom showy; the plant may be distinguished by the large coriaceous leaves with strong ill-spaced venation on the underside.

Cestrum megalophyllum is a widespread species, occurring from Venezuela and the Windward Islands west to Guatemala. It also occurs in ultramontane South America. This is a species of mature forests and deep shade, found in the lowlands and to at least 2,000 m in the Chiriquí mountains.

In the Amazon Basin and southward, *Cestrum megalophyllum* appears to be largely supplanted by *C. coriaceum* Schlecht. and *C. axillare* Vell. The first of these southern taxa has somewhat smaller but even stiffer leaves and a larger calyx, while the second has much smaller, thinner leaves. Extensive study of these southern populations may show that *C. megalophyllum* should best be considered as an infraspecific taxon under one of these species. *Cestrum axillare* is the earliest name of the three.

CANAL ZONE: On side road off Gaillard Highway 1 mi. NW of Summit Garden, *Blum et al. 2341, 2342* (DUKE). Near Madden Forest, *Candido 34* (DUKE, MO). Roadside, Madden Forest Road, 1, *Croat 8949* (MO). Radar Station Road 1 mi. N of Summit Gardens, *Croat 9071* (DUKE, MO). Pipeline Road near gate, *Croat 13939* (SCZ). Roadside in forest between Gatun and Fort Sherman, *Croat 15407* (MO). Just off Transisthmian Highway near Coco Solo Naval Hospital, *D'Arcy 5166* (F, G, MO, MPU, P). Madden Forest, side of disused gravel road, *D'Arcy 5245* (MO). Fort Sherman, U. S. Army Tropic Test Center Side, *Dwyer & Robyns 139* (MO). Galena Point, *Dwyer 6687* (MO). Fort Sherman Site, U. S. Army Tropic Test Center, *Dwyer 8589* (MO). Chagres, *Fendler 195* (GH, MO, US). *Foster 1065* (DUKE). Río Providencia at Fort Sherman, *Gentry 4842* (MO). Gatun, *Hayes 607* (NY). Without locality, *Johnston 1755* (A, MO). Around Gamboa, 29–100 m, *Pittier 2609* (C, GH). Road from Fort Sherman to Fort San Lorenzo, *Tyson & Blum 3753* (DUKE, MO). Barro Colorado Island, *Croat 5109, 5682, 8023, 9135, 9543, 10325, 14568, 15152* (all MO); *Ebinger 140* (MO, US); *Wilson 100* (F, MO). CHIRIQUÍ: Vicinity of Cerro Punta, 2,000 m, *Allen 1559* (GH, MO, NY, US). Finca Collins, vicinity of Boquete, *Blum & Dwyer 2529A*, (MO). Bajo Chorro, Boquete District, 6,000 ft, *Davidson 98* (A, MO, US). Between Pinola and divide on Chiriquicito-Caldera Trail, mostly in mossy forest, *Kirkbride & Duke 848* (MO). Cerro Vaca, in forest or thickets, 900–1,136 m, *Pittier 5315* (GH, NY). Chiriquí Viejo Valley, *White 104* (GH, MO, US). Chiriquí Viejo Valley near El Volcán, *White 221* (GH, MO). COCLÉ: Vicinity of El Valle, 600–1,000 m, *Allen 1191* (GH, MO, US). COLÓN: Near Río Piedras along road to Portobelo, *Blum et al. 2500* (DUKE). Forested area near Guasimo along river, *Croat 9973* (MO). Near bridge over Río Buenaventura near Portobelo, *Foster 1697* (DUKE). DARIÉN: 1–3 mi. SE of Santa Fé on Pan American Highway, Río Sabana, *Duke 4115* (GH, MO). Loma Piriaque, *Duke 8086* (OS). Near Refugio, 15–21 mi. N of Santa Fé, *Duke 10310* (OS). Río Cuasi, main stream 0–2.5 mi. S of Tres Bocas, *Kirkbride & Duke 1131* (MO). Caná and vicinity, 200–6,500 ft, *Williams 843* (NY, US). LOS SANTOS: Guayabo, W of Tonosi, *Stern et al. 1900* (MO, US). VERAGUAS: Mountains 3.9–5 mi. N of Santa Fé, *Gentry 2950* (MO).

12. **Cestrum nocturnum** L., Sp. Pl. 191. 1753. TYPE: Hort. Cliff. (BM, not seen).

Shrub or *tree* to 5 m tall, sometimes scandent; twigs green, minutely puberulent, very leafy. *Leaves* to 11 cm long, ovate, sometimes broadly so, apically acute or acuminate, basally rounded or obtuse, fine puberulent when emerging, glabrous with maturity; petioles ca. 1 cm long; minor leaves mostly wanting. *Inflorescences* several, axillary or terminal, mostly many-flowered, congested, sparingly branched panicles; peduncle slender with scattered leafy bracts; pedicels short with linear-lanceolate bracteoles 2–3 mm long. *Flowers* strongly night-scented, calyx 2 mm long, campanulate, fine puberulent inside and out, the lobes acuminate, enlarging slightly and becoming costate and mucronulate in fruit; corolla greenish or yellowish white, drying yellowish, the tube slender, 14–17 mm long, glabrous outside, sometimes pilose inside at the point of filament insertion; stamens equal, the filaments ca. 3 mm free, distinctly dentate at or just below the point of insertion, mostly glabrous; stigma slightly exserted. *Fruit* a hard or juicy black berry, elliptical or slightly obovoid, to 10 mm long.

The mostly glabrous corolla and prominent tooth-like appendages on the filaments are good features for recognition. Some Panamanian specimens have flowers much smaller than those found in other regions.

Cestrum nocturnum is widely grown in tropical gardens for its nocturnal scent. The type locality is Jamaica, and the species is native to the Antilles and parts of Central America, including lowland Panama. "Dama de noche."

BOCAS DEL TORO: Research Grounds, region of Almirante, *Cooper 409* (F, US). Río Teribe between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 478* (MO). Changuinola to 5 mi. S at junction of Río Changuinola and Río Teribe, 100–200 ft, edge of river and railway and adjacent rain forest, *Lewis et al. 814* (GH, MO, PMA, US). Without locality, *von Wedel 421* (GH, MO). CANAL ZONE: Drowned forest of upper Río Pequení between Salamanca Hydrographic Station and Río Boquerón, 70 m, *Allen 17277* (MO). Barro Colorado Island, *Bangham 429* (F, US). Colón and Empire, *Crawford 446* (NY). Fort Amador on causeway and islands, *Tyson 2025* (FSU, MO). CHIRIQUÍ: Río Macho de Monte, 1 mi. E of Cuesta de Piedra 2,800 ft, *Tyson 895* (FSU). COLÓN: Portobelo, *Holdridge 6399A* (MO, PMA). PANAMÁ: Piria, *Duke 1444* (OS).

13. **Cestrum pittieri** Francey, Candollea 6: 385–6. 1935. SYNTYPE: Costa Rica, *Tonduz s.n.* (US).

Ill-scented *shrub* or *tree* to 8 m tall; twigs stout, glabrous. *Leaves* to 18 cm long, elliptical, apically acuminate, basally obtuse or short acuminate, margins minutely revolute, coriaceous and minutely puberulent on the lamina beneath, veins 7–10 on each side, prominent beneath when mature; petioles 12–20 mm long, stout; minor leaves wanting. *Inflorescences* many, distributed along the branches, axillary, subumbellate clusters on pubescent, ebracteate, mostly unbranched peduncles 5–8 mm long; pedicels ca. 1 mm long, bracteoles 3–5 mm long, lanceolate. *Flowers* small, the calyx 3 mm long, short-tubular, puberulent outside and along the costae within, costate in the upper half, the lobes acuminate, unequal; corolla greenish, the tube 12 mm long, glabrous and glandular within, expanded at the apex, the lobes narrow, 3 mm long; stamens equal, the filaments 2 mm free, geniculate and with one or two large, 0.5 mm long, tooth-like appendages at the point of insertion, glabrous except for a few hairs near the teeth; stigma slightly exserted or at the mouth of the tube. *Fruit* (Francey) ellipsoid, 1-seeded.

The coriaceous leaves with strong venation beneath and the appendages on the filaments serve to distinguish this species. It differs from *C. megalophyllum*, with which it might be confused, in that the leaves are mostly broadest below the middle, and the base is not narrowed or attenuate.

This species is known only from Costa Rica and western Panama.

CHIRIQUÍ: Vicinity of David, 30–80 m, *Pittier 3366* (GH, US). LOS SANTOS: Guayabo, several mi. W of Tonosí, second growth riverine vegetation, *Stern et al. 1900* (MO, US).

14. **Cestrum racemosum** R. & P., Fl. Peru. 2: 29, *tab. 154.* 1799. TYPE: Peru, *Ruiz s.n.* (F).—FIG. 5.

C. mathewsii Dun. *in* DC., Prodr. 13(1): 637. 1852. TYPE: Peru, *Mathews s.n.* (US).
C. panamense Standl., Jour. Washington Acad. Sci. 15: 460. 1925. TYPE: Panama, Panamá, Río Tapia, *Standley 28042* (US).
C. grande Pittier, Jour. Washington Acad. Sci. 22: 32. 1932. TYPE: Venezuela, *Pittier 10393* (NY).

FIGURE 5. *Cestrum racemosum* R. & P.—A. Flowering branch (× ⅓). [After *Croat 6454* (MO).]—B. Fruiting branch (× ⅓). [After *Dwyer 4003* (MO).]

C. racemosum var. *grande* (Pittier) Francey, Candollea 6: 275. 1935.
C. racemosum var. *panamense* (Standl.) Francey, Candollea 6: 274–5. 1935.
C. racemosum var. *bolivianum* Francey, Candollea 6: 274–5. 1935. TYPE: Bolivia, *Steinbach 7259* (MO).

Shrub or *tree* to 12 m tall; twigs green, slender, glabrous. *Leaves* mostly 10–15 cm long, ovate or elliptical, oblique, apically acute or acuminate, basally rounded or obtuse, the margins sometimes revolute, soft membranaceous, dark

green, glabrous when mature, the veins many, evenly spaced and arcuate on each side of the midrib, raised and conspicuous beneath; petioles short, to 2 cm long; minor leaves absent. *Inflorescences* many, congested, distributed along the branches, axillary or terminal; peduncles short, to 3 cm long, angled, mostly unbranched, lengthening to 9 cm in fruit; pedicels to 4 mm long with linear, 1 mm long bracteoles. *Flowers* with the calyx ca. 3 mm long, cyathiform, campanulate or short tubular, prominently costate or not, pubescent or glabrous outside, glabrous within, short-lobed; corolla yellowish or greenish, sometimes purple blotched, the tube 10 mm long, slender, opening gradually to the apex, glabrous outside, inside glabrous or pubescent, sometimes tomentose at the base, the lobes 3–4 mm long; stamens equal, the filaments 1.5–3 mm free, smooth and straight, often pubescent below, not tumid, barbellate or appendaged; stigma included. *Fruit* black, ca. 6 mm long, obovoid.

The many parallel arcuate veins which stand out on the leaf undersides and the lack of pubescence on the mature leaves and corolla exterior are good characters for recognition of this species.

Cestrum racemosum is one of the common and widespread species of *Cestrum* in tropical America. It ranges from Brazil to British Honduras and perhaps beyond. A plant of stream sides and forest edges, it is found at lower and middle elevations and ascends to middle elevations in Chiriquí Province.

BOCAS DEL TORO: Region of Almirante, Farm 8 pasture, *Cooper 574* (F). Changuinola Valley, *Dunlap 579* (F, US). Zigla road at junction of Changuinola and Tuibe rivers, along wet bank of Changuinola, *Lazor et al. 2544* (FSU). Changuinola to 5 mi. S at junction of Ríos Changuinola and Teribe, 100–200 ft, edge of river and railway, and adjacent rain forest, *Lewis et al. 847* (MO). Vicinity of Chiriquí Lagoon, *von Wedel 1257* (GH, MO). Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel 2192* (GH, MO, US). CANAL ZONE: Pipeline Road 4.4 mi. NW of gate, *Croat 12753* (MO). Roadside near Río Pedro Miguel, Madden Forest, *D'Arcy 5160* (ADW, BIRM, C, F, MO, MPU, PMA, UCWI), *5160B* (MO). Madden Forest, side of disused gravel road, *D'Arcy 5246* (MO). Gatún, *Dwyer 1777* (MO). Madden Dam, *Dwyer 4003* (MO). Between Summit and Gamboa, *Greenman & Greenman 5218* (MO). Barro Colorado Island, *Bailey & Bailey 159* (F); *Croat 6454* (DUKE, MO), *7386* (MO), *8899* (DUKE, MO, NY); *Ebinger 298* (MO, US). CHIRIQUÍ: Above Paseo la Canoa, 3,100 ft, *D'Arcy 5432* (MO). Along Río Dupí near sea level, *Pittier 5238* (NY). COCLÉ: Near El Valle de Antón, *Croat 13284* (MO). Cloud forest at La Mesa above El Valle, *Croat 13415* (MO, SCZ). Cerro Pilón above El Valle, *Croat 14325* (MO). Near El Valle, cloud forest on slopes of Cerro Pilón, *Duke 12188* (F, MO, OS). Between Cerro Pilón and El Valle de Antón, 700–900 m, cloud forest, *Duke & Dwyer 13892* (G, MO, MPU, W). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7960, 7970* (both MO), *7980* (C, F, G, MO, MPU, PMA, WIS). COLÓN: Vicinity of Guasimo on Río Miguel de la Borda, *Croat 10000* (SCZ). María Chiquita, E of Río Piedras toward Portobelo, thickets near beach, *Dwyer & Kirkbride 7770* (COL, DUKE, MO, NY, SCZ, UC). Salud, *Lao & Holdridge 185* (MO, PMA). DARIÉN: 0–2 mi. E of Tres Bocas, along the shortest headwater of Río Cuasi, *Kirkbridge & Duke 1185* (MO). Manene to the mouth of the Río Cuasi, *Kirkbridge & Bristan 1497* (MO). Vicinity of Yaviza along Río Chucunaque, along Inter-American Highway between Pinogana and Yaviza, 1 km from Tuira, *Stern et al. 130* (MO). PANAMÁ: Tocumen near airport, *Dwyer 4060* (MO). Along Río Pacora, 200 m downstream from bridge of Carretera Interamericana, *Nee & Mori 3629* (MO).

15. **Cestrum reflexum** Sendt. *in* Mart., Fl. Bras. 10: 218. 1846. TYPE: Bolivia, *d'Orbigny 659* (not seen).—FIG. 6.

C. floribundum Britt., Mem. Torrey Bot. Club 6: 92. 1896, non Willd. *ex* R. & S., Syst. Veg. 4: 807. 1819. SYNTYPES: Bolivia, *Bang 1200, 1470* (both NY).

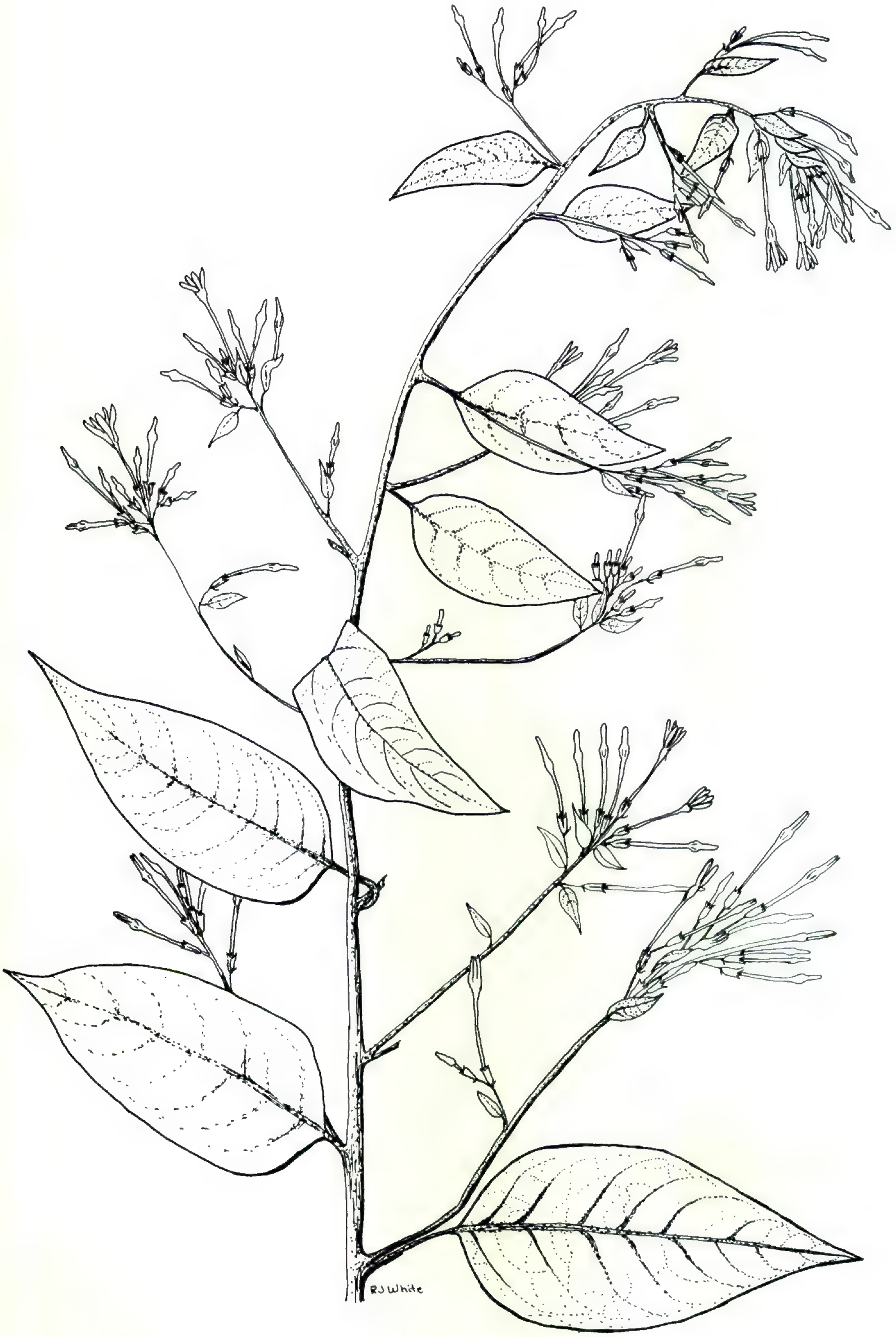

FIGURE 6. *Cestrum reflexum* Sendt., flowering branch ($\times \frac{3}{5}$). [After *von Wedel 1657* (MO).]

Shrub or woody *vine* to 2 m; twigs slender, puberulent in longitudinal lines. *Leaves* to 14 cm long, ovate, apically acute, basally rounded or obtuse, 7–12 on each side, puberulent along the veins on both sides and beneath with scattered short hairs on the lamina; drying with a grey-brown cast; petioles 1–1.5 cm long, puberulent; minor leaves mostly wanting. *Inflorescence* terminal or axillary, a long-stalked, many-flowered open panicle, the peduncles to 10 cm long, puberulent, more so near the apex, bracts to 1 cm long, oblong, scattered but larger, broader and more numerous on terminal inflorescences; flowers sessile in the axils of short stalked bracteoles, the bracteoles 1–2 mm long or sometimes foliose and ovate and reaching 10 mm long, puberulent. *Flowers* conspicuous, the calyx 3–4 mm long, tubular, puberulent outside, the lobes short-deltoid, tomentose outside and pubescent near the apex within, becoming 5–7 mm long in fruit; corolla greenish white, the tube 20–25 mm long, slender, expanded slightly near the apex, glabrous inside and out; stamens subequal, the filaments 1 mm free, straight, edentate, glabrous; style pubescent near the apex, the stigma included. *Fruit* ovoid, glistening black, 9–12 mm long.

This species is superficially a close match for *C. scandens*. The greyish-brown rather than green or yellowish cast to the leaves when dried, the sessile flowers, puberulent veins and peduncles, accrescent calyx, glabrous corolla tube, longer separation of filaments from the corolla tube and the shape of the bracteoles are all useful characters.

Cestrum reflexum is a plant of the lowlands, ranging from Brazil and Ecuador to Costa Rica. It is not reported for Venezuela or for the Windward Islands. In Panama most collections are from Bocas del Toro but it has also been found in Darién. "Wild jasmine" (English).

BOCAS DEL TORO: Common vine or trailer, *Carleton 100* (US). Region of Almirante, research grounds, *Cooper 90* (NY), *151* (US). Lower Changuinola, *Stork 60-1/2* (US). Lower Changuinola, common along railway tracks, *Stork 280* (US). Vicinity of Chiriquí Lagoon, Water Valley, vine, flowers green, *von Wedel 1537*, *1657*, *1712* (all GH, MO, US). DARIÉN: Trail between Cana and Boca de Cupe, Cana, Río San José below former goldmine headquarters, *Stern et al. 637* (GH, MO, US). Boca de Cupé, *Williams 676* (NY).

16. **Cestrum rugulosum** Francey, Candollea 7: 78–9. 1936. TYPE: Costa Rica, *Pittier 872* (US).

Shrub to 3(–5), m tall; twigs glabrous. *Leaves* 12–20 cm long, ovate, elliptic or oblong, often oblique, apically mostly acute or acuminate, basally rounded or obtuse, the margins slightly revolute, above puberulent on the midvein and major lateral veins and with scattered, minute glandular hairs on the lamina, beneath with minute hairs on the major and minor veins, lateral veins 15–20 on each side, prominently elevated beneath, the surface often drying dark with a rugose surface; petioles puberulent, 2–3 mm long; minor leaves wanting. *Inflorescences* numerous, scattered along the stems, axillary and terminal racemes or small panicles on mostly unbranched, short or elongate, pubescent to glabrate axes to 4 cm long, leafy bracts scattered through the inflorescences; pedicels to 5 mm long, slender, drying black, the bracteoles linear, 1.5 mm long. *Flowers* fragrant, calyx 2–3 mm long, cyathiform or campanulate, puberulent, almost ecostate,

elongating slightly in fruit, the teeth short, deltoid, unequal, corolla cream-colored, often with some purplish or blackish markings, the tube 25–28 mm long, opening gradually to the apex, glabrous to manifestly pubescent outside, inside pilose at the base and sometimes puberulent along the length of the tube, the lobes 3 mm long, lanceolate; stamens equal, the filaments 3–5 mm free, barbellate and sometimes dentate at the point of insertion, glabrous to pilose below, the stigma included. *Fruit* bright, matte-white, globose, flattened apically, juicy, ca. 10 mm across; seeds 1–10, 4.5 mm long, brown or black.

While variable in technical characters, plants seen in the field look remarkably uniform. Superficially like small shrubs of *C. racemosum*, *C. rugulosum* can be distinguished by the pubescence on the leaf undersides, the filaments and often the outside of the corolla. On dried material, the dark, usually blotched appearance of the leaves is distinctive.

Cestrum rugulosum is plentiful above the town of Cerro Punta in Chiriquí Province at about 2,500 m. Outside of the Chiriquí mountains it ranges into cloud forests in Costa Rica.

Two anomalous fruiting collections resemble *C. rugulosum* on the herbarium sheet, but they may not be this species. They differ in having elongate, stramineous inflorescence axes. In the following citations, these are identified by an asterisk (*).

CHIRIQUÍ: Cerro Punta ca. 7,000 ft, flowers white, *Blum et al. 2419* (FSU, MO, SCZ). Finca Collins, near Boquete, *Blum & Dwyer 2529A* (DUKE). Disturbed cloud forest at Monte Rey above Boquete, *Croat 15737** (MO). Plentiful above Cerro Punta, 7,600 ft, *D'Arcy 5346* (MO). Above Cerro Punta, 7,600 ft, *D'Arcy 5360* (MO). Above Cerro Punta, 7,600 ft, *D'Arcy 5362* (MO). Above Cerro Punta, 6,300 ft, *D'Arcy 5375, 5376* (MO). Chiquero, Boquete District, 5,500 ft, *Davidson 558* (A, MO, US). Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7748** (MO). Chiriquí Viejo Valley, Cerro Punta, *White 33* (GH, MO). Valley of the upper Río Chiriquí Viejo, *White 329* (MO, US).

17. **Cestrum scandens** Vahl, Eclog. Amer. 1: 24. 1796. TYPE: *von Rohr s.n.*, herb. Vahl (C; MO, photo; IDC 2201. 9: II. 6).

Scandent *shrub*, sometimes several m long; twigs slender, glabrous. *Leaves* to 10 cm long, ovate, apically acute, basally obtuse or rounded, the margins slightly revolute, veins 4–7 on each side, membranaceous, glabrous; petioles subsessile to 3.5 cm long; minor leaves sometimes present, rotund to lanceolate. *Inflorescences* several, elongate open panicles, axillary or terminal, the peduncle to 15 cm long, slender, glabrous, with foliaceous bracts near the base, the pedicels to 2 mm long, stout, the bracteoles linear, to 2 mm long. *Flowers* with the calyx 3 mm long, tubular-campanulate, green, puberulent in the upper half, strongly costate, the teeth short-deltoid and evenly pubescent within; corolla green, the tube 18–20 mm long, slender, expanding slightly below the apex, outside glabrous, inside pubescent at the base or glabrous, the lobes lanceolate, 7–9 mm long; stamens equal, the filaments free less than 0.5 mm, glabrous, straight, unappendaged, the style pubescent on the upper 2 mm, the stigma laterally flattened. *Fruit* (Francey) blue, obovoid, 9 mm long, 8-seeded.

This species closely resembles *C. reflexum* but is distinguishable on a number of inconspicuous characters. The flowers are pedicellate, i.e. the bracteole is

located midway up the stalk, and in fruit the base of the pedicel becomes slightly swollen at the bracteole node. In general the leaves of *C. scandens* tend to dry yellowish or green and not greyish-brown as in *C. reflexum.*

One collection, *Piper 5707* (US), differs from others in that the inflorescence is strictly terminal at the end of large, leafy branches which are foliaceous to the summit. It does not seem to differ otherwise from *C. scandens. Cestrum terminale* (Dun.) Pittier or *C. scandens* var. *terminale* Dun. also has terminal inflorescences, but the branches on the type material seen (*Brotero s.n.*, MO, photo) are not leafy to the top.

Cestrum scandens is a scandent vine of the lowlands, occurring from Venezuela to Guatemala. In Panama it is apparently rare.

CANAL ZONE: Juan Mina, *Piper 5707* (US). Río Agua Salud near Frijoles, *Piper 5869* (US). COCLÉ: Penonomé and vicinity, 50–1,000 ft, *Williams 399* (NY, US). PANAMÁ: Algarobó, Río Gatún, shrub, *Hayes 389* (NY). Panamá, *Hayes 458* (NY). Weedy sandbar with *Ricinus communis* and partly planted to bananas, along Río Pacora, 1 km upstream from Pacora, *Nee & Mori 3626* (MO). Along Corozal Road near Panamá, moist forest, *Standley 26852* (US). Juan Diaz, moist woods, *Standley 30455* (US).

18. **Cestrum standleyi** Francey, Candollea 6: 249–250. 1935. TYPE: Costa Rica, *Standley & Valerio 48082* (F, US).

Shrub or *tree* to 7 m tall; twigs glabrous. *Leaves* variable in size, 5–15 mm long, elliptic or ovate, apically acute or acuminate, basally obtuse, margins slightly revolute, the venation obscure, veins few, 5–6 on each side of the midvein and almost perpendicular to it, upper surface often drying dark; petioles to 1.5 cm, stout, drying black; minor leaves wanting. *Inflorescences* numerous, scattered along the stems, axillary or arising from enlarged leaf scars, sub-umbellate at the end of short, slender glabrate peduncles, 15 mm long; pedicels short or wanting, the bracteoles linear-lanceolate, 4 mm long. *Flowers* with the calyx 1.5–3 mm long, tubular, puberulent outside, glabrous within, the tube contracted above the ovary, strongly costate to almost ecostate, irregularly 2–5-lobed, the lobes puberulent; corolla tube 12–14 mm long, slender, glabrous inside and out, expanded near the apex, the lobes 4 mm long, narrowly obtuse; stamens unequal, the filaments 1.5 mm free, straight, glabrous, unappendaged. *Fruit* (Francey) oblong, green, 9 mm long.

This species and *C. johnniegentrianum* have manifestly smaller flowers than other species of *Cestrum* occurring in Panama, both in length and diameter. The obscure venation, which is nearly at right angles to the midvein, and the tubular, often constricted calyx are characters for recognition of *C. standleyi.* The flowers on the type collection are slightly smaller and the calyx is less contracted than on the Panamanian material seen.

Cestrum standleyi occurs at middle and upper elevations in wet forests. It ranges from Panama into Costa Rica, where it is known only from the type collection.

COCLÉ: La Mesa near El Valle, 2,000 ft, *Dwyer & Duke 8269* (MO). PANAMÁ: Road to Cerro Jefe, 2–3 mi. S of Goofy Lake, 2,000–2,200 ft, lower elevations of cloud forest, *Lewis et al. 266* (MO).

19. **Cestrum strigilatum** R. & P., Fl. Peru. 2: 29, *tab. 156.* 1799. TYPE: Peru, *Ruiz s.n.* (?B, HAL, neither seen).

C. calycinum Willd. *in* R. & S., Syst. Veg. 4: 808. 1819. TYPE: (not seen).

Shrub or small *tree* to 4 m tall; twigs tomentose with yellowish or brownish dendritic hairs. *Leaves* elliptic, to 25 cm long, thin, apically acute, basally rounded or obtuse, above glabrate with obscure venation, beneath tomentose and the venation elevated and prominent; petiole ca. 1.5 cm long. *Inflorescences* short, axillary, racemose, the peduncle to 5 cm long, tomentose; pedicels wanting, bracteoles short and scale-like or leaf-like and almost as long as the calyx. *Flowers* with the calyx 8–12 mm long, tubular, pubescent, lobed ¼–⅓ way down, the lobes lanceolate, strongly angled, unequal; corolla greenish-yellow, the tube ca. 25 mm long, slender, gradually expanded apically, tomentose outside, inside pubescent in the upper portion, the lobes slender, ca. 7 mm long; stamens equal, the filaments ca. 1 mm free, glabrous or pubescent and slightly tumid near the point of insertion, not appendaged; the style puberulent in the upper portion. *Fruit*[12] 10–12 mm long, ellipsoidal, dark violet.

This species is distinctive in its tomentose twigs, leaf undersides, and corollas. The hairs are dentritic, and the flowers are elongate and slender.

Although type material was not seen, examination of a range of material cited by Francey argues for considering *C. strigilatum* and *C. calycinum* as the same species.

Cestrum strigilatum is a South American species ranging to Brazil and Peru. It is known in Panama from only one collection.

PANAMÁ: Ca. 12 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3809* (F, MO).

20. **Cestrum warszewiczii** Klotsch, Allgem. Gartenzeit. 19: 362. 1851. TYPE: Costa Rica, *Warszewicz 1738* (not seen).

C aurantiacum var. *warszewiczii* (Klotch) Francey, Candollea 6: 103. 1936.
C. aurantiacum var. *macrocalyx* Francey, Candollea 6: 105. 1936. TYPE: Not designated.

Tree to 7 m tall; twigs puberulent. *Leaves* to 7 cm long, elliptic, oblique, the veins conspicuously reticulate beneath when dry, glabrous; petioles to 2 cm long. *Inflorescence* a large, many-flowered, terminal panicle to 25 cm long, the peduncles stout, drying with sharp angles; pedicels short and stout. *Flowers* showy; calyx tubular, 12 mm long, the tube strongly angled, the lobes 3–5 mm long, linear lanceolate; corolla orange, the tube 20 mm long, the lobes ca. 5 mm long, narrowly ovate. *Fruit* white, enveloped by the fruiting calyx, the fruiting pedicels stout.

With its bright orange or yellowish flowers and white fruits enveloped by the calyx tube, *C. warszewiczii* is distinct from other Panamanian species. The single specimen does not permit examination of androecium or gynoecium.

Francey considered this species conspecific with *C. aurantiacum* Lindl., but

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[12] Panamanian material seen is without fruit, and this portion of the description is taken from Francey, Candollea 6: 139, 143.

examination of a range of specimens from Central America at the Smithsonian Institution (US), showed that on specimens from Mexico and Guatemala, the range of *C. aurantiacum*, the fruit is not enveloped by the calyx.

CHIRIQUÍ: Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 41* (MO).

6. CYPHOMANDRA

Cyphomandra Mart. *ex* Sendt., Flora 28: 161–176, *tab. 1–9*. 1845. TYPE: *Solanum sycocarpum* Mart. & Sendt.

Cyathostyles Schott *ex* Meissn., Gen. Pl. Comm. 184. 1840, nomen nudum.
Pionandra Miers, London Jour. Bot. 4: 353. 1845. TYPE: Not designated.
Pallavicinia De Not., Flora 30: 567. 1847. TYPE: *Cyphomandra fragrans* Sendt.

Unarmed *shrubs*, *trees* or *vines*, sometimes foetid, pubescent with simple or dendritic hairs. *Leaves* simple or compound, entire or lobed, often cordate at the base, sometimes dimorphic; petioles sometimes clasping the stem; minor leaves present or not. *Inflorescences* often at a dichotomy of the stem, simple or branched racemes, often secund and conspicuously circinnate; peduncles sometimes clasping; pedicels articulating at the base, usually leaving a prominent cicatrix of pedicel scars. *Flowers* mostly 5-merous, calyces campanulate with obtuse or obsolete lobes; corollas deeply or shallowly lobed, often with membranaceous plicae of different texture or color; filaments free or connate, mostly short, extending into an elaborate connective which may shield the dorsal surface of the thecae or part of it, the anthers opening by 2 small, sometimes confluent terminal pores and sometimes ultimately longitudinally; ovary glabrous or not, often conical or elongate, 2-loculed, the ovules many, anatropous on enlarged axile placentae, the style slender, the stigma small. *Fruit* a fleshy or juicy berry; seeds flattened, the embryo circinnate at the periphery of the seed.

This genus resembles sect. *Leiodendra* of *Solanum*, from which it is distinguished mainly by the elaboration of the anther connective. The position of the inflorescence differs in the two groups, and the often cordate leaf base and the large fleshy, pendant fruits of *Cyphomandra* are often distinctive. The generic distinction between *Solanum* and *Cyphomandra* is not sharp and requires clarification. In some species, the connective is only slightly elaborated, and it may be difficult without histological techniques to determine whether or not it is in fact elaborated. A consideration of a wide range of *Cyphomandra* morphology will be necessary to establish the generic distinctions. Among the Panamanian species, *Solanum eshbaughianum*, and *S. granelianum* warrant clear examination as to generic placement.

Cyphomandra includes 50–60 species, mainly of ultramontane South America. Some species are used by man for food. *Cyphomandra crassicaulis* (Ort.) Kuntze (= *C. betacea*) is a food crop in Australia and New Zealand and in some parts of South America under the name "tree tomato." *Cyphomandra crassicaulis* has been reported from Panama. No specimens have been seen to support these reports, but it is possible that this species has been cultivated from time to time. It resembles *C. hartwegii*, but the leaves are thicker and the indumentum is dense; the fruit is much larger.

R. B. Dressler, Smithsonian Tropical Research Institute, has indicated in conversation that *C. hartwegii* is pollinated by male euglossine bees (*Eulaema bombiformis*). He remarked that in Brazil, where *Cyphomandra* has its greatest species diversity, the euglossines do not occur. Even in the many species of *Cyphomandra* with well-elaborated anther connectives the gross structure of the flowers is quite diverse, and that of *C. hartwegii* with its elongate, pendulous flowers and treelike form is an extreme attained in the northern members of the genus. In Brazil and the Andes, the flowers are often quite different from this in overall appearance and different pollinators might be expected. The three species found in Panama are very different-looking, and it would be useful to document their pollinators. The role, if any, of the expanded connective in encouraging pollination is unknown. It may be a remnant of the leaf-blade from which the stamen was modified.

Cyphomandra takes its name from the Greek "kyphos" = curve, and "andra" = masculine, referring to the anthers.

a. Leaves pinnately compound, peduncles elongate ..... 2. *C. diversifolia*
aa. Leaves simple, peduncles various.
  b. Inflorescence an elongate, circinnate, many-flowered cincinnus, the peduncle to 15 cm long; fruit ca. 3 cm long ..... 3. *C. hartwegii*
  bb. Inflorescence a short, 1–6-flowered raceme, the peduncle 1–2 cm long; fruit ca. 2 cm long ..... 1. *C. allophyllum*

1. **Cyphomandra allophylla** (Miers) Hemsl., Biol. Centr. Amer. Bot. 2: 417. 1882.

Pionandra allophylla Miers *in* Seem., Bot. Voy. Herald 174–5. 1854. TYPE: Panama, *Seeman 169* (BM, K; MO, photo).
Solanum ellipsoideibaccatum Bitt., Fedde Repert. 11: 486. 1913. TYPE: Colombia, *Smith 1153* (NY).
S. *ellipsoideibaccatum* var. *ficilobum* Bitt., Fedde Repert. 13: 173. 1914. TYPE: Panama, Chiriquí, near San Félix, *Pittier 5237* (US).
S. *allophyllum* (Miers) Standl., Jour. Washington Acad. Sci. 17: 16. 1927.

Glabrate, erect, branched *herb* to 1 m tall with fistulose stems. *Leaves* entire, three- or five-lobed, often all on the same plant, entire leaves mostly 5–6 cm long and 3–4 cm broad, broadly ovate, rounded at the base, acuminate at the apex, the lobed leaves 9–11 cm long and 6–10 cm broad, the sinuses broadly rounded, approaching the midvein, glabrate with scattered hairs on the lamina, silvery beneath when fresh; petioles 1.5–5 cm long, slender, narrowly winged. *Inflorescence* a short, 1–6-flowered raceme at a dichotomy of the stem, the peduncle 1–2 cm long, glabrous, drying stramineous; pedicels ca. 1 cm long, broadening sharply into the calyx. *Flowers* inconspicuous, calyx 2 mm long, lobed about halfway, the lobes deltoid, hardly accrescent in fruit, glabrous; corolla white or yellowish, 10–12 mm long, lobed about halfway; filaments affixed to the dorsal surface of a membranaceous ring inserted near the base of the corolla tube, ca. 1 mm long, about half its length consisting of an expansion visible from the dorsal side of the anther, the anthers lanceolate, ca. 6 mm long, acuminate apically with 2 small terminal pores surmounted by conspicuous rims; ovary elongate-conical, the stigma punctiform. *Fruit* ripening white, ca. 2 cm long, ellipsoid, immature fruits striped or not; seeds yellow, ca. 1.5 mm long, compressed.

This species is distinctive in its widely lobed leaves, lack of pubescence, and the short stramineous peduncles bearing large fleshy fruits. Collections seen are all from the Pacific lowlands of eastern and central Panama.

The connective enlargement is small and easily overlooked. The nature of the fruit and the position of the inflorescence are those of the genus *Cyphomandra*. Many of the petioles have somewhat clasping bases.

CANAL ZONE: Vicinity of Cerro Viejo on K16C, *Blum 1263* (MO). Farfan Beach from Thatcher Highway to Palo Seco, scrub above sandy beach, *Burch et al. 1410* (MO). Gatun, *Hayes 563* (NY). Vicinity of Madden Dam, disturbed forest, *Lewis et al. 27* (ADW, BIRM, F, MO, MPU). Madden Forest Preserve along Las Cruces Trail and highway, deep rain forest, roadside weed, *Lewis et al. 5315* (MO, MPU). Howard Air Force Base near Red Devil drop zone, disturbed area, *Tyson 1854* (MO). Barro Colorado Island, *Zetek 5040* (MO). DARIÉN: Vicinity of Pinogana, 20 m, *Allen 939* (F, GH, MO, NY, US). Near mouth of Río Yape, *Allen 326* (MO). PANAMÁ: 6 mi. from Chepo on Pan American Highway, wooded areas, *Duke 4091, 4092* (both MO). Vicinity of El Llano *Duke 5798* (MO). Hills ca. 2 mi. E of El Llano, *Foster & Kennedy 1973* (DUKE). Near Juan Diaz, in field, 25 m, *Killip 3100* (MO). Along Tapia river, dense forest, 75 m, *Killip 3154* (MO). Sabanas, NE of Panama City, *Bro. Paul 175* (GH). Chepo, *Pittier 4689* (US). WITHOUT LOCALITY: *Seeman 169* (BM, K).

2. **Cyphomandra diversifolia** (Dun.) Bitt., Fedde Repert. 17: 354. 1921.

Solanum diversifolium H. & B. *ex* Dun., Sol. Syn. 8. 1813. TYPE: Venezuela, herb. H. & B. (P).

Cyphomandra caracasana (R. & S.) Sendt., Flora 11: 168. 1845.

Solanum caracasanum R. & S. *in* L., Syst. Veg. 4: 664. 1819. TYPE: Venezuela, *Bredemeyer s.n.* (?B, not seen; MO, photo).

Cyphomandra caudata Standl., Trop. Woods 16: 25. 1928, nomen nudum; Publ. Field Columbian Mus., Bot. ser. 4: 258. 1929. TYPE: Panama, *Cooper 398* (F, NY).

Small *tree* 3 m tall; twigs slender, green, pilose with simple hairs to 2 mm long. *Leaves* pinnately 4–7 compound, the leaflets entire, obovate or ovate, the terminal leaflet largest, reaching 20 cm long, the apex acuminate or caudate, the base obtuse, the veins 3–6 on each side of the midvein, both sides with scattered long hairs on the veins and lamina; petiolules ca. 2 mm long; petioles to 2.4 cm long; minor leaves wanting. *Inflorescence* to 15 cm long, an elongate, pendant panicle or cyme of several slender, secund racemes, the peduncles glabrous, the pedicels filiform, ca. 10 mm long. *Flowers* purplish in bud; calyx 1–2 mm long, subtruncate, puberulent; corolla ca. 10 mm long and apparently quite broad, lobed ⅔ the way down with well-developed plicae, densely puberulent outside; stamens equal, ca. 5 mm long, the filaments free, stout, ca. 1 mm long, the connective massive, extending as a boss from base to apex on the back of the anther, the filament and connective drying dark, the thecae the same size or smaller than the connective, not drying dark, the anthers dehiscing by 2 terminal pores on the elongate apex of the thecae and tardily by longitudinal slits near the base and near the apex; ovary glabrous, elongate-conical, the style glabrous, expanding upwards to the flattened stigma, exceeding the anthers and about equalling the corolla lobes. *Fruit* an ellipsoid or ovoid fleshy berry to ca. 3 cm long; seeds many, 3–4 mm long.

Cyphomandra diversifolia bears a strong resemblance to *C. cornigera* Dun. *in* DC. (Prodr., 13(1): 401) as figured by Smith & Downs (Solanaceae *In* P. R. Reitz, Fl. Illustr. Catarin. *tab. 30* 1966), but the anther connective of *C.*

diversifolia is much more elaborated, and its leaflets are much smaller and less membranaceous. Rare in Panama, this species is similar in overall appearance and in the general structure of the fruit and flower to a number of South American species. Further study of the genus may show that its range extends into the ultramontane South America. "Wild cucumber."

BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper* 398 (F, NY).

3. **Cyphomandra hartwegii** (Miers) Dun. *in* DC., Prodr. 13(1): 401. 1852.—FIG. 7.

Pionandra hartwegii Miers, London Jour. Bot. 4: 363. 1845. TYPE: Colombia-Ecuador, *Hartweg 1297* (BM, G, K; GH, MO, photos).

Cyphomandra heterophylla Donn. Sm., Bot. Gaz. (Crawfordsville) 27: 436. 1899, non Taub., Bot. Jahrb. Syst. 15, Beibl. 38: 16. 1893. SYNTYPES: *Donn. Sm. 6670*, *Pittier 9059*, *10294*, *Tonduz 1146*, *Cooper 10215*, all Costa Rica (all US).

C. costaricensis Donn. Sm., Enum. Pl. Guatem. 6: 84. 1903. TYPE: Based on *C. heterophylla* Donn. Sm.

C. artocarpophylla H. Winkl., Fedde Repert. 7: 246. 1909. TYPE: Bolivia, *Buchtien 1444* (M, US).

C. dendroidea Pittier, Contr. U. S. Natl. Herb. 13: 116. 1910. TYPE: Colombia, *Pittier 512* (US).

C. holtonii Hochr., Bull. New York Bot. Gard. 6: 285. 1910. TYPE: Colombia, *Holton 555* (G, K, NY; MO, photo).

C. mollicella Standl., Publ. Field Columbian Mus., Bot. ser. 4: 322. 1929. TYPE: Honduras, *Standley 54720* (F, US; MO, photo).

C. tobagoensis Sandw., Kew Bull. 1938: 370. TYPE: Tobago, *Broadway 3879* (US).

Foetid *shrub* or small *tree* to 4(–12) m tall; twigs mostly angled, fine-puberulent, slender. *Leaves* drying dark, to 30 cm long, mostly cordate but sometimes (especially turoins or juveniles) deeply or sinuately pinnately lobed or toothed, above glabrous or with minute stout hairs, beneath softly puberulent with short acicular hairs, the margins ciliate; petioles to 10 cm long, puberulent; minor leaves often present, resembling the major leaves. *Inflorescence* subterminal or at a dichotomy of the stem, an elongate, several-flowered, little-branched, pendant raceme to 15 cm long, the peduncle with a prominent cicatrix of pedicel scars, conspicuously circinnate in unfolding, the pedicels to 2 cm long, slender, puberulent, articulating at the base. *Flowers* elongate and dull-colored; calyx ca. 2 mm long, cyathiform, subtruncate with short-deltoid umbos, puberulent, corolla 1–2 cm long, lobed nearly to the base, the lobes lanceolate, becoming strongly reflexed, puberulent inside and out, greenish, greyish, yellowish or brownish, whitish puberulent on the margins; stamens ½–⅘ as long as the corolla lobes, the filaments free and glabrous, the anthers ca. 10 mm long, lanceolate, the thick, puberulent, violet or brown connective covering the dorsal surface, the yellow thecae puberulent in the distal portion, opening by 2 minute, confluent, terminal pores; ovary elongate-conical, glabrous, the style exceeding the anthers by 2–3 mm but shorter than the corolla lobes, the stigma small and globose. *Fruit* an ellipsoid, fleshy berry ca. 3 cm long, longitudinally striped, green or brownish but perhaps yellow when fully ripe; seeds many, compressed, light-colored, ca. 5 mm long.

This is an almost characteristic shrub of second growth woods in lowland central Panama, occurring at lower and middle elevations. It is easily recognized

FIGURE 7. *Cyphomandra hartwegii* (Miers) Dun.—A. Flowering branch (× ½). [After *Dwyer 9485* (MO).]—B. Leaf (× 3/5). [After *D'Arcy 3973* (MO).]

in the field by its large, cordate, foetid, textilous leaves. It ranges from Honduras east to Brazil and Bolivia. The slender, elongate flowers, pendant inflorescences and large connectives are extreme within the genus.

Duke and Porter (*Darien Ethnobotanical Dictionary*, 1970) report that in

Darién, this species is used by humans for food and is known as "contra gallinazo." For a note on pollination, see under the generic description above.

BOCAS DEL TORO: Without locality, *Dunlap 264* (K). Almirante just N of Dos Milla, *McDaniel 5122* (MO). Vicinity of Chiriquí Lagoon, *von Wedel 1080, 2404* (GH, MO, US). Water Valley, Chiriquí Lagoon, *von Wedel 1835* (GH, MO, US). Old Bank Island, *von Wedel 1900* (GH, MO, US). CANAL ZONE: Secondary growth found growing in bananas, Gatun Lake, *Close*, 1925 (US). Barro Colorado Island, *Bailey & Bailey 302* (F, GH); *Croat 9016* (DUKE, MO, NY), *10196, 11774, 12934, 16579* (all MO); *Ebinger 605* (GH, MO, US); *Foster 1784* (DUKE); *Kenoyer 511* (US); *Killip 39968* (MO, NY); *Luteyn & Croat 905* (DUKE); *Shattuck 653* (F, MO, US); *Wetmore & Abbe 82* (F, GH, MO); *Zetek 3658* (F), *3912* (F, MO), *Z-4979* (F, MO, US). CHIRIQUÍ: San Bartolo Limite, 19 km W of Puerto Armuelles, *Busey 613* (BIRM, MO). Progreso, *Cooper & Slater 181* (US). COCLÉ: Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12167* (DUKE, MO, NY, OS). COLÓN: East Santa Rita Ridge, *Correa & Dressler 1050* (DUKE, MO, PMA). Zona maderera de Santa Rita, 15 km NE de la Carretera Transistmica, *Correa & Dressler 1132* (DUKE, MO, PMA). Santa Rita Ridge, *Croat 13835* (MO). Santa Rita Ridge ca. 4–5.5 mi. E of Transisthmian Highway, advanced secondary forest, *Lewis et al. 5293* (DUKE, MO, PMA). DARIÉN: Vicinity of Pinogana, ca. 20 m, *Allen 919* (GH, MO, NY, US). Between Quebrada Venado and Peje Swamp on the headwaters of Río Tuqueza, *Bristan 1009* (MO). 1–3 mi. SE of Santa Fé on Pan Am Highway, Río Sabana, *Duke 4107* (MO). 2–3 mi. SE of El Real, *Duke 4847* (GH, MO, PMA, US). Between Pucro and Río Punusa along Pan American Highway, *Duke 5396* (GH, MO). Río Pirre, *Duke 8283* (OS). Cuipo forest near Santa Fé, *Duke 12896* (MO, US, WIS). Between Paya and Palo de las Letras, *Duke & Kirkbride 14026* (MO). Santa Fé, University of Georgia Cuipo Forest, site no. 2, ca. 15 m, *Duke 14260* (F, MO). Vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuqueza, *Stern et al. 817* (G, GH, MO, OS). Near Marraganti, *Williams 647* (NY). Near Cana, 2,000–6,500 ft, *Williams 959* (NY). PANAMÁ: E slope of Cerro Jefe, 2,700 ft, *Blum & Duke 2192* (MO). Forest near dam site S of Cañita, *Croat 14508* (MO, SCZ). Cerro Jefe, *D'Arcy 3949* (ADW, MEXU, P, W, WIS), *3958* (ADW, BIRM, C, F, MO, MPU, PMA, UC, WI), *3973* (MO). Roadside, Santa Rita Ridge, *D'Arcy & D'Arcy 6131* (MO). Cerro Jefe region, second growth thicket by road, *Dressler 3070* (DUKE, MO, PMA). Road to 8 mi. S of Goofy Lake toward Cerro Jefe, *Dwyer 7065A* (MO). Cerro Jefe, *Dwyer & Gentry 9485* (MO). E slope of Cerro Jefe, 2,700–3,000 ft, *Tyson et al. 3356* (MO). SAN BLAS: Road between Mandinga and Cangandi, *Duke 14739* (OS).

7. DATURA

Datura [Pona] L., Sp. Pl. 179. 1753; Gen. Pl., ed. 5. 83. 1754. TYPE: *D. stramonium* L.

[*Datura Turcarum Garziae* Pona, Desc. Montis Baldi *in* Clus., Rar. Pl. Hist., Litt. 328. 1601].
Stramonium Mill., Gard. Dict., abr. ed. 4. 1754. TYPE: Not designated.
Apemon Raf., Fl. Tell. 2: 11. 1837. TYPE: *A. crassicaule* Raf. (= *Datura ceratocaulos* Ort.).
Ceratocaulos Bern. *ex* Reichb., Handb. 201. 1837. TYPE: *Datura ceratocaulos* Ort.

Unarmed, ephemeral or perennial *herbs* or *shrubs*, sometimes foetid, pubescence of mostly simple, sometimes viscid hairs; twigs stout or slender. *Leaves* simple and entire, repand or variously pinnately lobed or toothed, petiolate; minor leaves present and resembling the major leaves. *Flowers* solitary (sometimes aggregated) on erect or pendulous pedicels; calyx tubular, sometimes inflated and sometimes appressed to the corolla tube, prefloration complete and floral egress mostly by 5 valvate teeth, the tube then circumscissile near the base leaving a flange which may enlarge into a shield or cup subtending the fruit; corolla funnelform, tubiform or almost tubular, mostly white or purplish, flaccid, glabrous or variously pubescent, the limb 5- or 10-lobed, sometimes double or triple; stamens equal, the filaments inserted near the middle of the tube or

lower, variously pubescent, the anthers oblong and slightly curved, basifixed, dehiscing longitudinally, free; ovary conical, 4-loculed by proliferation of the placentae, the ovules many, the stigma variously shaped. *Fruit* a leathery 4-celled capsule, mostly locucidally dehiscent terminally to about halfway down, usually covered with soft or woody spines, more or less globose; seeds large, mostly black, flattened and roughened; embryo circinnate in fleshy endosperm.

A genus of about ten species of warm temperate regions in both New and Old Worlds. Eight species are native to Mexico and the southern United States, which region may be considered a center of speciation. Commonly occurring as ruderal weeds, one species of Mexico is paludal. Some species are nocturnally scented.

Plants in this genus contain the alkaloids atropine, hyoscyamine, scopolamine, and others closely related which are common to the drugs bella-donna, hyoscyamus, stramonium, etc., of various pharmacopoeas. Alkaloids are found in several parts of the plants. Leaves are smoked in some countries and are used as catoplasms to reduce pain or swelling. The seeds are in some places a traditional method of criminal poisoning. Unlike the alkaloids of tobacco, those of *Datura* (and of *Brugmansia*) in the quantities obtained from single seeds or puffs of smoke may produce drastic or violent reactions. The lethal dose may be small. In some countries there is elaborate ritual centering around these plants. In Panama, one species is occasionally cultivated for ornament and the other, known only from one collection, is commonly a ruderal weed in other countries. The climate of Panama may be too moist for establishment of this genus in a wild state.

The name is a Latin corruption of "Dutra," an Indian name for *Datura stramonium*.

Useful reference:

Safford, W. D. Synopsis of the genus *Datura*. Jour. Washington Acad. Sci. 11: 173–182. 1921.

a. Fruit inclined or nodding, not dehiscing regularly, and covered with stout spines or bumps; cultivated ornamental ..... 1. *D. metel*

aa. Fruit erect, dehiscing by 4 valves, and covered with slender spines; ruderal weed ..... 2. *D. stramonium*

1. **Datura metel** L., Sp. Pl. 179. 1753. TYPE: Hort. Cliff. 55.2 (BM).—FIG. 8.

D. fastuosa L., Syst., ed. 10. 2: 932. 1759. TYPE: LINN 243.3, (not seen; NY, photo).

Glabrate *shrub* to 2 m tall; twigs dark, purplish-colored (Panama). *Leaves* broadly ovate, to 15 cm long, margins subentire to repand-dentate, the base truncate or obtuse and oblique, the lamina with scattered small hairs; petioles slender, 3–8 cm long. *Pedicels* stout, erect or nodding, ca. 10 mm long, tardily deciduous at the base. *Flowers* with the calyx tubular, little or not inflated, slightly wider at base and apex, 3–8 cm long, opening by 5 subequal lobes 1–2 cm long, circumscissile near the base leaving a distinct flange 5–15 mm long, glabrous or puberulent with short, simple hairs, drying with prominent longitudinal veins; corolla showy white or purple, tubiform, the narrowly obconical

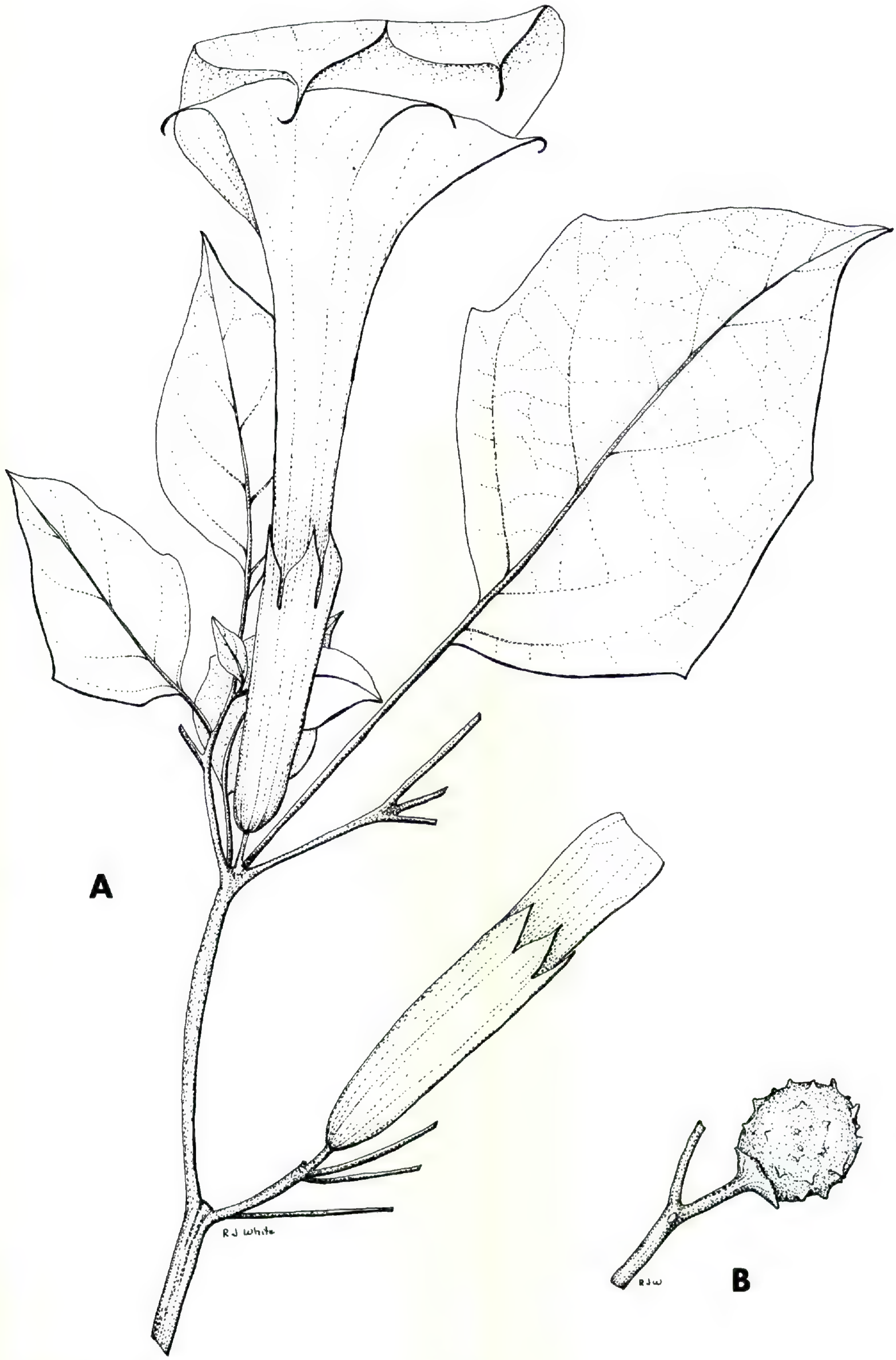

FIGURE 8. *Datura metel* L.—A. Flowering branch (× 3/5).—B. Fruit (× 3/5). [After *D'Arcy 5480* (MO).]

tube filling the calyx, 8–20 cm long, the limb sometimes double or triple, flaring to 3–10 cm across, sinuately 5-lobed with 5 or 10 linear teeth; filaments glabrous, sometimes connate or apically appendaged, anthers ca. 10 mm long; ovary short-conical, style glabrous. *Fruit* ovoid or elliptical to 4 cm long, splitting irregularly, covered with conspicuous tubercles or soft, stout teeth, 4-loculed, many seeded, nodding to somewhat upright but not strictly erect; seeds flattened, reniform, ca. 5 mm long, with a small fleshy aril.

First described from southeast Asia and east Africa, *D. metel* is cultivated in the tropics and indoors in temperate regions. The single locality in Chiriquí where this species has been collected is below 350 m elevation; however, residents of the Volcán District (1,200–2,000 m) say that a purple "floripondio" was occasionally cultivated there many years ago. They may be referring to this species.

A member of a genus normally considered to be herbaceous, *Datura metel* is capable of becoming shrubby and quite woody at the base. The Panamanian specimen cited here was 2 m tall and spreading across 1 m in the crown.

CHIRIQUÍ: In garden, Gualaca, *D'Arcy 5480* (MO).

2. **Datura stramonium** L., Sp. Pl. 179. 1753. TYPE: Hort. Cliff. 55.1 (BM).

Short-lived perennial or ephemeral *herb*, to 1 m tall, stems green or purplish. *Leaves* mostly repand-dentate, the teeth acuminate, the base often dimidiate, glabrate to pubescent with small, simple, multicelled, pulverulent hairs, the petioles less than half as long as the blades. *Pedicels* mostly erect, stout, 5–10 mm long. *Flowers* sometimes showy; calyx tubular, ca. 5 cm long, puberulent, slightly wider at the base, opening by 5 lanceolate-acuminate teeth ca. 5 mm long, circumscissile near the base leaving a distinct flange ca. 5 mm long; corolla showy, white (Panama) or purple, tubiform, 6–8 cm long, about twice as long as the calyx, the limb with 5 subulate 4–5 mm long teeth; anthers 3–4 mm long, ellipsoid. *Fruit* erect, ovoid, 2 cm long, covered with slender, stiff, ascending spines, 4-loculed, many seeded, dehiscing to near the base by the apical sutures.

This species is distinctive in its prominently toothed leaves, erect, herbaceous habit, and in the long erect tubular flowers followed by erect, spiny capsules.

The above description is taken from the sole Panamanian collection. Plants from other areas are larger in most dimensions.

Datura stramonium is distributed in many countries as a weed.

CANAL ZONE: Mindi, *Cowell 178* (NY).

8. DEPREA

Deprea Raf., Sylv. Tell. 57. 1838. TYPE: *Physalis orinocensis* Kunth (= *Deprea orinocensis* (Kunth) Raf.).

Herbs or *shrubs*, with simple, perhaps viscid hairs. *Leaves* membranaceous, entire or nearly so; pedicels slender; minor leaves present or not. *Inflorescences* axillary, one to many flowered, fascicled on the stem; peduncle not evident,

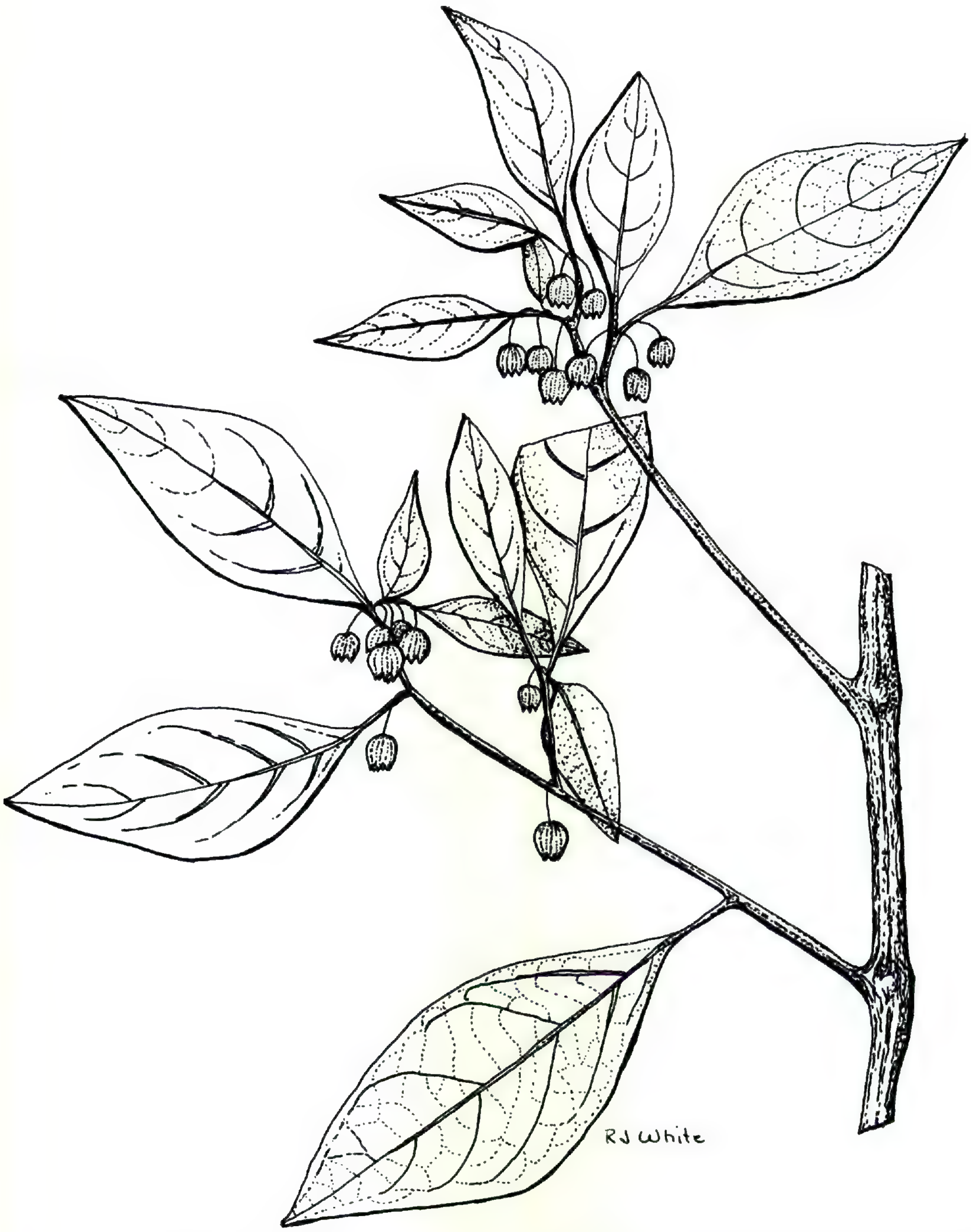

FIGURE 9. *Deprea orinocensis* (Kunth) Raf., fruiting branch (× 1). [After *Wilbur 15367* (MO).]

pedicels slender. *Flowers* small, the calyx campanulate to cyathiform with 5 short, narrow teeth extending from major veins of the limb, the sinuses squarrose and not splitting, giving the calyx a truncate appearance, in fruit enlarging to loosely envelop the fruit, the base with no indication of invagination, the teeth not enlarging; the corolla campanulate, 5-lobed; the stamens 5, equal, the fila-

ments inserted near the top of the corolla tube, the anthers oblong, dehiscing longitudinally, slightly exserted. *Fruit* a berry loosely enveloped by the accrescent calyx.

This genus is doubtfully distinct from *Physalis*, differing mainly in the lobed corolla and in the truncate appearance of the calyx. Dried material looks significantly different from that of most species of *Physalis* because of the absence of evagination in the base of the calyx, but there are a number of *Physalis* species which have this appearance.

The name *Athenaea*, based on *Witheringia picta* Mart., is conserved over *Deprea* Raf., based on *Physalis orinocensis* Kunth. and *P. xalapensis* Kunth. The two Kunth species (type material at P) are congeneric with one another but not with *Witheringia picta*, which has a calyx unequally lobed nearly to the base, a condition quite different from that found in the Kunth species.

1. **Deprea orinocensis** (Kunth) Raf., Sylv. Tell. 57. 1838.—FIG. 9.

Physalis orinocensis Kunth *in* H. & B., Nov. Gen. 3: 12–13. 1818. TYPE: Venezuela, *Bonpland s.n.* (P).
Larnax orinocensis (Kunth) Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 38. 1849.
Withania orinocensis (Kunth) Dun. *in* DC., Prodr. 13(1): 455. 1852.
Athenaea orinocensis (Kunth) D'Arcy, Phytologia 25: 116. 1973.

Weak *shrub* or *herb* to 1.5 m tall, stems puberulent to villous with short, soft, simple hairs which flatten and crumple on drying. *Leaves* elliptical to ovate, mostly 6–8 mm long, apically acute or acuminate, basally acute or obtuse, often oblique, membranaceous, glabate on both sides, the major veins puberulent; petioles slender, to 18 mm long. *Inflorescence* a few-flowered fascicle or solitary, axillary, pedicels filiform, puberulent, ca. 3 mm long in flower, becoming 5–7 mm long and remaining slender in fruit. *Flowers* small, the calyx 1 mm long, subtruncate with 5 minute apical teeth, puberulent, in fruit becoming 7–9 mm long, ovoid, loosely enveloping the fruit; the corolla blackish purple, campanulate, puberulent, lobed about halfway down, the lobes obtuse, the margins short ciliate; the anthers ca. 1 mm long, oblong, slightly exserted. *Fruit* globose, ca. 5 mm across.

This species is similar to *D. xalapensis* (Kunth) Raf. of Mexico, which has larger fruits, generally more pubescent leaves and pedicels. The calyx teeth of *D. xalapensis* are also broader and deeper.

CHIRIQUÍ: Ca. 2 mi. E of Cerro Punta on trailside in the Quebrado Bajo Grande, 6,900 ft, *Wilbur & Teeri 13132* (Duke).

9. JALTOMATA

Jaltomata Schlecht., Index Seminum Hort. Hal. 1838: 8. 1838. TYPE: *J. edulis* Schlecht. = *J. procumbens* (Cav.) J. L. Gentry.

Jaltomata Schlecht., Linnaea 13: Litt. 98. 1839. TYPE: *J. edulis* Schlecht.
Jaltonia Steud., Nom., ed. 2. 1: 797. 1840. TYPE: *J. edulis* Schlecht.
Saracha sensu auct., non R. & P., Fl. Peru. Prodr. 31, 34. 1794. TYPE: S. *punctata* R. & P.

Herbs, erect or spreading, unarmed, hairs simple, often glandular. *Leaves* ovate or elliptic, entire or mostly toothed, glabrate or viscid, membranaceous, often with large minor leaves. *Inflorescence* solitary, a slender peduncled umbel situated at a dichotomy of the stem. *Flowers* with the calyx lobes folded over the bud, becoming erect or outward-curved, deltoid-obtuse, accrescent, spreading, and subtending but not enclosing the fruit; corolla rotate or broadly campanulate, lobed to about halfway, the lobes broad, deltoid; filaments exserted, slender, inserted near the base of the corolla, mostly pubescent, anthers short, dehiscing longitudinally; ovary glabrous, viscid, situated on a disc, 2-loculed, the style slender, the stigma small. *Fruit* a globose, many-seeded, mucilaginous berry, the surface sometimes viscid; seeds compressed-lenticular, the embryo curved around the endosperm at the periphery of the seed.

A genus of a few species ranging throughout tropical America, *Jaltomata* is the vernacular Mexican name for the plants.

1. **Jaltomata procumbens** (Cav.) J. L. Gentry, Phytologia 26: 123. 1973.—FIG. 10.

Atropa procumbens Cav., Ic. Descr. Pl. 53, *tab.* 72. 1791. TYPE: (not seen).
Saracha procumbens (Cav.) R. & P., Fl. Peru. Prodr. 2: 43, *tab. 180b*. 1794.
Bellinia procumbens (Cav.) R. & S. *in* L. Syst. Veg. 4: 56, Introd.; 687. 1819.
Saracha nitida Bitt., Fedde Repert. 19: 265. 1924. TYPE: Venezuela, *Fendler 1007* (MO, NY).

Herb to 2 m tall; stems fistulose, green, glabrate to viscid pubescent with straight hairs which dry white. *Leaves* ovate, entire or sparingly sinuate-dentate, apically acuminate, basally obtuse or narrowed, above glabrate, beneath sparingly pubescent along the veins, the petioles to ca. 5 cm long, often winged by the narrowed leaf base; minor leaves often present and as large as the majors. *Inflorescence* an umbel on a slender, puberulent, unbranched peduncle, to 4 cm long, pedicels filiform, 1 cm long, to 3 cm long in fruit. *Flowers* mostly deflected, calyx 2–3 mm long, lobed about halfway down, accrescent and becoming 1 cm long in fruit, with a conspicuous midvein, spreading and not enveloping the fruit; corolla yellow to greenish white, often with some greenish dots, 10–15 mm across, lobed about halfway, the lobes deltoid or obtuse; anthers ellipsoid, ca. 2 mm long; style expanded-capitate. *Fruit* a black mucilagineous berry, 8–10 mm across. Seeds many, compressed lenticular, ca. 1 mm long. Chromosomes $n = 12$.

This species is found from Mexico to the Andes, but to judge from collections in herbaria, it is not a plentiful plant. In Panama it is common in the Chiriquí mountains in cafetales and at the edges of fields. "Uchuba negra" (Colombia), "yerba-mora" (Colombia).

BOCAS DEL TORO: Robalo Trail, N slope of Cerro Horqueta, 6–7,000 ft, *Allen 4916* (MO). CHIRIQUÍ: In cafetal, Los Naranjos, *D'Arcy 4270* (MO). Stream bank, Nueva Suisa, Volcan District, 5,700 ft, *D'Arcy 5309* (ADW, MPU). On dead log above Nueva Suisa, Volcan District, 6,000 ft, *D'Arcy 5317* (MO). In cafetal just above Boquete, *D'Arcy & D'Arcy 6472*

FIGURE 10. *Jaltomata procumbens* (Cav.) J. L. Gentry, fruiting branch (× 3/5). [After *Dwyer 6961A* (MO).]

(MO). Clearing in rain forest, Bajo Corro, Boquete District, 6,000 ft, *Davidson 415* (MO, US). Cerro Horqueta, *Dwyer 6961A* (MO). COCLÉ: Disturbed forest edges, hills NE of El Valle de Antón, 2,000 ft, *Lewis et al. 1702* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1287* (MO).

10. JUANULLOA

Juanulloa R. & P., Fl. Peru. Prod. 27, *tab. 4.* 1794. TYPE: *J. parasitica* R. & P.

Ulloa Pers., Syn. 1: 218. 1805. TYPE: *Juanulloa parasitica* R. & P.
Laureria Schlecht., Linnaea 8: 513. 1833. TYPE: *L. mexicana* Schlecht.
Portaea Tenore, Agli Sci. Ital. 7 Congr. 902. 1845. TYPE: *P. aurantiaca* Tenore.
Sarcophysa Miers, Ann. Mag. Nat. Hist., ser. 2. 3: 166. 1849, nomen; 4: 190–1. 1849. TYPE: *S. speciosa* Miers (= *Juanulloa speciosa* (Miers) Dun. *in* DC.).

Unarmed *shrubs*, mostly growing as hemi-epiphytes or doubtfully as parasites, often high in the forest canopy; the ends of the twigs often an expanded cicatrix from fallen leaves or inflorescences. *Leaves* simple, entire, of moderate size, glabrous to tomentose with dendritic hairs; minor leaves wanting. *Inflorescence* an open or congested variously branched panicle not exceeding the leaves, or sometimes reduced to a short raceme or spike, the peduncles and pedicels mostly stout and not elongating greatly in fruit. *Flowers* sometimes showy, calyx cam-

panulate, angled, sometimes fleshy, splitting halfway or more into 5 or fewer oblong or lanceolate lobes, mostly dendritic-pubescent outside; corolla bud somewhat pointed apically and slightly imbricate, when expanded mostly yellow, red or orange, tubular, slightly curved or saccate in the upper portion, slightly contracted at the apex with 5 short, deltoid or obtuse lobes, tomentose outside, sometimes pubescent within; stamens 5, equal, included or slightly exserted, inserted low in the tube, sometimes pilose and geniculate at the point of insertion, straight above the base, the anthers elongate, dehiscing by longitudinal slits, 4-thecate with a short apicule of mostly connective tissue; ovary superior in an annular, perigynous disc, ovoid, 2-loculed with many ovules, the stigma small. *Fruit* a many-seeded ovoid berry which does not exceed the calyx lobes; seeds flattened, with a slightly or strongly curved embryo.

As now constituted, *Juanulloa* includes about 10 species ranging from Mexico (Chiapas, Veracruz) to Colombia, Peru, and Equador. Collections have been taken from near sea level to 2,400 m in Colombia. These are seldom-collected plants, and there are few specimens in herbaria, probably because they are unnoticed or inaccessible in the treetops. The narrowly tubular, pubescent flowers separate *Juanulloa* from *Markea*, *Solanum*, *Lycianthes*, and *Solandra*, the solanaceous genera commonly occurring as hemi-epiphytes or treetop climbers in Panama.

Material from Pavon of *J. parasitica* R. & P., the type species, was seen at the British Museum (BM) and designated as lectotype. Material at Montpellier (MPU) and some at the British Museum labelled *J. parasitica* is not this genus. No material was found at Madrid (MA).

A few species are cultivated as novelties in temperate greenhouses. The genus takes its name from Jorge Juan, 1713–1773, and Antonio Ulloa, 1716–1795, botanists who travelled Peru and Ecuador.

Useful reference:

Cuatrecasas, J. The Colombian species of *Juanulloa*. Brittonia 10: 146–150. 1958.

1. **Juanulloa mexicana** (Schlecht.) Miers, Ann. Mag. Nat. Hist., Ser. 2. 4: 188. 1849.—Fig. 11.

Laureria mexicana Schlecht., Linnaea 8: 513. 1833. TYPE: (not seen).
Juanulloa panamensis Miers, Ann. & Mag. Nat. Hist., ser. 2. 4: 190. 1849; Illustr. S. Amer. Pl. 2: 41, *tab. 46*. 1857. TYPE: David, Veraguas, Costa Rica [Chiriquí, Panama], *Seemann 1200* (BM; MO, photo).
J. sargii Donn. Sm., Bot. Gaz. (Crawfordsville) 18: 5, *tab. 1*. 1893. TYPE: Guatemala, *Donnell Smith 1467* (GH, MO, NY, US).
J. bicolor Gleason, Phytologia, 1: 37. 1933. TYPE: *Lawrance 435* (A, NY, US).

Vine or *shrub*, hemi-epiphytic; twigs drying a greenish buff color, irregularly striated and scaling. *Leaves* elliptic or oblong, to 20 cm long, broadest above the middle, coriaceous, smooth but with scattered echinoid or dendritic hairs on the midrib and lamina above, densely whitish fine-tomentose and perhaps glabrescent beneath; petioles channeled above, glabrous to densely pubescent.

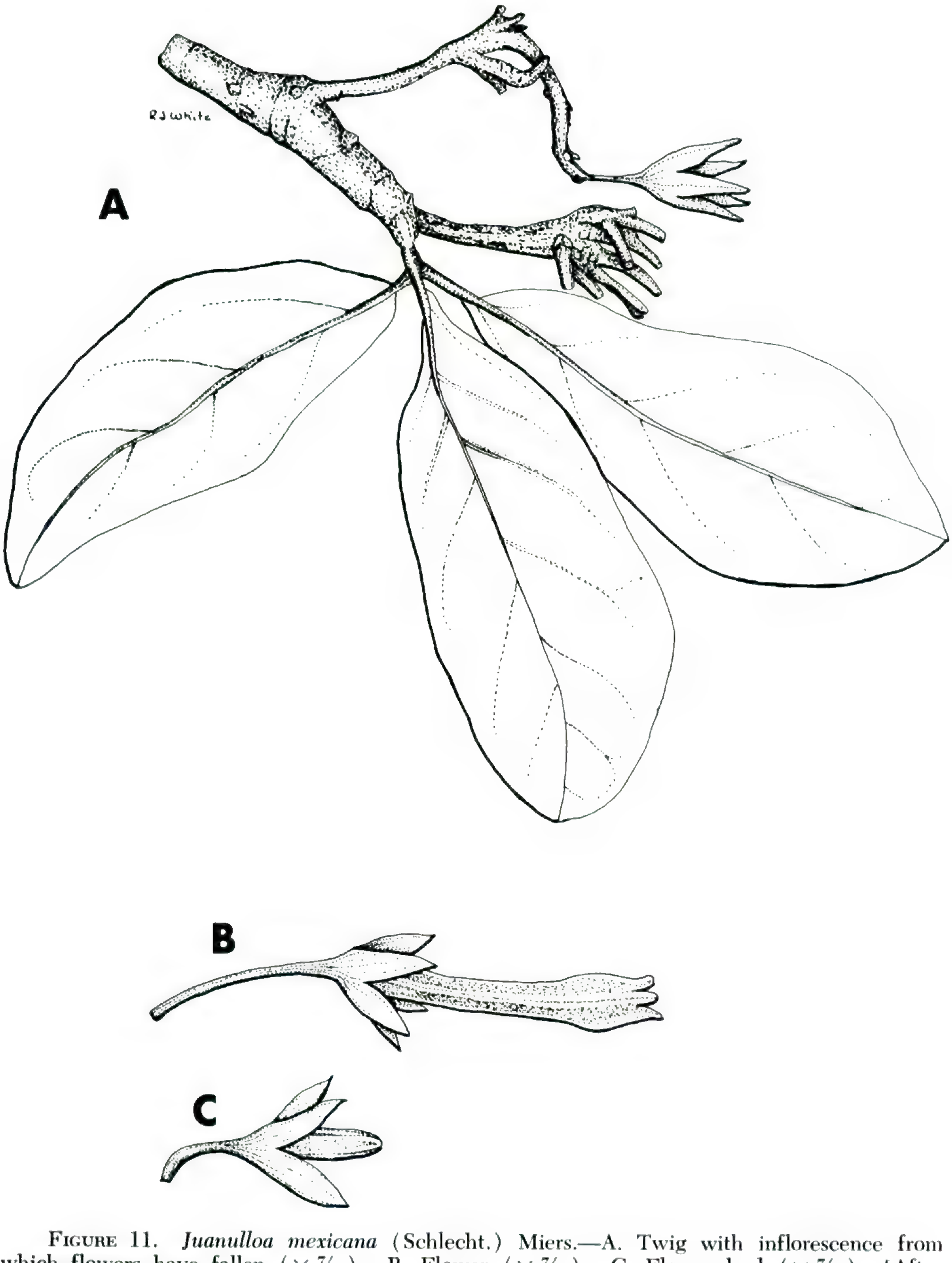

FIGURE 11. *Juanulloa mexicana* (Schlecht.) Miers.—A. Twig with inflorescence from which flowers have fallen (× 7/10).—B. Flower (× 7/10).—C. Flower bud (× 7/10). [After *Yuncker et al.* 8823 (MO), Honduras.]

Inflorescence a contracted, subumbellate or corymbose panicle at the ends of branches; pedicels tomentose, 8–12 mm long. *Flowers* with the calyx 12–15 mm across at the base of the lobes, vestite outside with a yellow, orange or brownish, partly deciduous tomentum, split about halfway down into 5 ovate to oblong

lobes with acuminate tips and scattered hairs on the inside; corolla 3.5–4 cm long (Panama) and ca. 3 times as long as the calyx, tubular, conspicuously 5-ribbed or pleated, slightly expanded in the upper portion with a yellowish, stellate tomentum outside, glabrous within except for a villous area near the point of stamen insertion, the lobes ovate, ca. 5 mm long and glabrous within; stamens (*Skutch 3841* (US), Costa Rica) on slender filaments inserted 5–8 mm above the base of the corolla tube, glabrous except for a massive basal tuft of hairs at the base, the anthers partly exserted, elongate, ca. 10 mm long, 1.5 mm thick at the broadest point, dehiscing longitudinally, basally hastate and apically with a short point, the connective dorsally marked by a dark (?purple) line; style slender, flattened, the stigma small, ellipsoid, situated at the level of the anther tips. *Fruit* (*Allen 5519* (US), Costa Rica) a soft, conical or ovoid berry, 2 cm long, not exceeding the calyx lobes, the elongate slender style persistent; seeds large, reniform, 4–5 mm long.

Living material of this species was not seen. Collectors report the calyx is orange or yellow, and the corolla is reddish orange or dark brown. Panamanian collections have somewhat smaller flowers than those of most Costa Rican or Colombian collections, but they appear to be well within the range for the species as a whole.

Juanulloa ferruginea Cuatrec. of Colombia differs in having a conspicuous loose tomentum of large dendritic hairs on the petioles and leaf undersides, and it also has stout woody thickenings on the peduncles.

Juanulloa mexicana apparently ranges from Colombia (Antioquia) to Mexico. Most collections from Costa Rica are from areas of deciduous forest and were growing in full sun. Two of the three Panamanian collections, however, are from high rainfall areas of Bocas del Toro with forests sparingly or not deciduous.

BOCAS DEL TORO: Region of Almirante, Daytonia Farm, vine, *Cooper 209* (F). Upper Changuinola, Changuinola Valley, Sanchez Potrero, epiphytic, *Dunlap 585* (F, US). CHIRIQUÍ: David, *Seemann 1200* (BM).

11. LYCIANTHES

Lycianthes (Dun.) Hassl., Ann. Conserv. Jard. Genève 20: 173–183. 1917, nom. cons.

Otilix Raf., Med. Bot. 2: 87. 1828. TYPE: *Solanum lycioides* L. (*S. licioides*).
Solanum subsect. *Lycianthes* Dun. *in* DC., Prodr. 13(1): 29, 156–183. 1852. LECTOTYPE: *S. lycioides* L. (= *Lycianthes lycioides* (L.) Hassl.).
Parascopolia Baill., Hist. Pl. 9: 338. 1888. TYPE: *P. acapulcensis* Baill.

Herbs, *shrubs* or *vines*, mostly unarmed, glabrous or pubescent with various types of hairs.[4] *Leaves* simple, entire or nearly so; minor leaves often present. *Inflorescences* solitary or fascicled in the leaf axils, few to many-flowered. *Flowers* with the calyx campanulate or cyathiform, apically truncate, 10-ribbed, the ribs giving rise to 0–10 teeth lateral on the calyx wall near the summit of the calyx, the teeth mostly 5 or 10, when 10 then often appearing in 2 series, not splitting at the sinuses in flower or fruit; corolla rotate, 5-lobed to various depths, the interplicate area sometimes thickened; stamens mostly 5, equal or unequal,

the filaments inserted on the short corolla tube, the anthers elongate, opening by small terminal pores, sometimes connate, rarely pubescent; ovary 2-loculed, the ovules few to many on proliferated placentae. *Fruit* a dry, pulpy or juicy berry, globose, ovate, or pyriform, not enclosed in the sometimes enlarged calyx; seeds compressed-discoid, the embryo circinnate around the periphery of the seed, the endosperm fleshy.

The genus includes perhaps 200 species of mostly rare plants to judge from the small holdings in herbaria. Most species occur in tropical America, but a dozen or more species are found in the South Seas and in Asia. The Old World species appear to be very closely related to various American members of the genus. One or two species are occasionally cultivated for ornament, and a few may have local medicinal uses, but otherwise the genus is without known uses.

Lycianthes has traditionally been confused with *Solanum*. First proposed as a genus by Hassler, the group was greatly amplified shortly after by Bitter (1919). Both Hassler and Bitter, who were collaborating, considered stone cell concretions in the fruit to be of diagnostic significance in establishing the genus. Bitter further argued that the stone cell concretions are an indication of primitiveness, being rudiments of ancestral drupaceous condition. The largest and best developed stone cells in *Lycianthes* are in fruits of *L. acidochondra*, one of the most advanced members of the genus, and a *Lycianthes*-like fruit occurs in *Solanum dimidiatum* Raf. of the United States which is clearly far from the primitive stock of *Solanum*. Stone cell concretions are not given much taxonomic weight by modern botanists, and they are not believed to be generically or even specifically consistent as held by Bitter.

The nature of the *Lycianthes* calyx is of generic significance. Through fusion of the lateral veins leading from the traces vascularizing adjacent lobes and fusion of tissue of the sinuses, the calyx has become 10-ribbed and truncate at the apex. In many cases some or all of these ribs vascularize teeth of a secondary nature, which appear as enations of the calyx wall proximal to the truncate apex or sleeve. Sometimes these teeth are very long and slender, or in other cases thick and lignified, but in each case, the united portion of the calyx apex appears as a sleeve distal to the point of departure of the teeth. In still other cases, no lateral teeth are apparent, and the 10 ribs may not be superficially evident. The sleeve, or truncate calyx, and the frequent presence of 10 teeth are useful as field characters.

Reasons for the small number of collections of *Lycianthes* are not understood. Perhaps the plants do not bloom frequently. In any case, present collections are not sufficiently numerous to determine to a satisfactory degree the range of variation occurring within the various taxa of the genus.

Useful reference:

Bitter, G. Die Gattung *Lycianthes*. Abh. Naturwiss. Vereine Bremen 21: 292–520. 1919 [1920].

a. Leaf undersides and most parts of plant with stellate or dendritic pubescence; pubescence apparent to the naked eye.
b. Hairs of the upper leaf surface of simple, stout hairs ..... 8. *L. hygrophila*

bb. Hairs dendritic or stellate on both leaf surfaces and on stems.
c. Leaves glabrous or nearly so on the lamina beneath (veins mostly pubescent).
d. Leaves coriaceous, drying dark; teeth of fruiting calyx slender, elongate ..... 13. *L. tysoniana*
dd. Leaves membranaceous, not drying dark; teeth of fruiting calyx woody, stout, conical ..... 1. *L. acidochondra*
cc. Leaves evenly pubescent on the undersides.
e. Calyx teeth filiform, mostly puberulent, somewhat longer but not thicker in fruit ..... 6. *L. hawkesiana*
ee. Calyx teeth slender to stout, glabrous to tomentose, in fruit stouter, woody, at least basally.
f. Calyx teeth almost glabrous, becoming woody and stout, at least basally in fruit.
g. Calyx teeth becoming stout, conical, less than 4 mm long in fruit ..... 1. *L. acidochondra*
gg. Calyx teeth becoming elongate, stout basally but slender apically, more than 4 mm long ..... 5. *L. guianensis*
ff. Calyx teeth tomentose, not woody or much stouter in fruit.
h. Calyx teeth extending more than 3 mm beyond the sleeve, pubescence of calyx variously colored (sometimes gray), pedicles short or long.
i. Calyx teeth stout (by virtue of pubescence) in flower and fruit, corolla ca. 4 mm across in bud, pedicles stout, less than 10 mm long ..... 7. *L. howardiana*
ii. Calyx teeth slender (although pubescent) in flower, corolla ca. 7 mm across in bud; pedicles slender, more than 14 mm long ..... 11. *L. porteriana*
hh. Calyx teeth short, not extending more than 2 mm beyond the sleeve, pubescence of calyx yellowish or brown; pedicles more than 14 mm long (fruit) ..... 9. *L. luteynii*
aa. Plants with all simple hairs; pubescence often obscure to the naked eye.
j. Calyces pubescent with prominent, slender teeth.
k. Stems and leaves strigose with stramineous hairs 2–3 mm long ..... 2. *L. amatitlanensis*
kk. Stems and leaves appressed pubescent with fine hairs ..... 3. *L. beckneriana*
jj. Calyces glabrous, mostly without slender teeth but deltoid teeth or lateral umbos sometimes present.
l. Anthers less than 5 mm long, free.
m. Calyx 5–6 mm across with prominent, deltoid-acuminate teeth near the truncate apex ..... 10b. *L. maxonii* var. *grandidentata*
mm. Calyx mostly less than 4 mm across, teeth sometimes emerging at the sides of the calyx away from the truncate apex .. 10a *L. maxonii* var. *maxonii*
ll. Anthers more than 5 mm long, connate or tightly coherent.
n. Calyx less than 2 mm long in flower, becoming 4 mm long in fruit, the venation obscure ..... 12. *L. synanthera*
nn. Calyx 2–3 mm long in flower, 3–5 mm long in fruit, 10 ribs mostly evident in flower, when obscure then the flowering calyx more than 3 mm long ..... 4. *L. escuintlensis*

1. **Lycianthes acidochondra** (Bitt.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 341. 1919 [1920].

Solanum acidochondrum Bitt., Fedde Repert. 13: 98–100. (Jan.) 1914; Abh. Naturwiss. Vereine Bremen 23: 153, 5. 10 (Feb.) 1914. LECTOTYPE: Panama, *Fendler 197* (US; GH, MO, isolectotypes).

Clambering, woody *vine*; twigs grayish-ferrugineous with appressed, short-stalked, dendritic and stellate hairs. *Leaves* somewhat coriaceous or mem-

branaceous, broadly elliptical to 8 cm long, obtuse at each end, the margins sometimes slightly revolute, soon glabrate above, evenly and softly pubescent beneath with stalked stellae, rarely glabrate, veins mostly 3 on each side of the midvein; petioles mostly 5–20 mm long, often reddish tomentose. *Inflorescence* solitary or a few-flowered fascicle, the pedicels slender becoming woody, glabrate to fine tomentose, 2–3 cm long, not much longer in fruit. *Flowers* inconspicuous, the calyx ca. 10 mm across, sparingly pubescent with small stellate or sub-simple hairs, glabrescent, the 10 teeth only slightly unequal, thickened and obtuse; the corolla greenish white, 15–18 mm long, the interplicae thickened, with short, simple or stellate hairs outside; stamens unequal, one anther 5.5 mm long, the 4 others 2.3 mm long and tightly coherent, with a few short sub-stellate or simple hairs inside; the ovary subglobose-conical, 3 × 2.5 mm, glabrous, the style 9.5 mm long, slightly exserted, glabrous. *Fruit* juicy, globose, ca. 20 mm across, the calyx teeth becoming stout, woody, pyramidal, the cup drying reflexed from the fruit; seeds compressed discoid, 4–5 mm across with a distinct, thickened margin.

This species with its overall ferrugineous tomentum, greenish-yellow flowers and heavy, reflexed fruiting calyces is quite unlike any other Panamanian species. Most collections are from the Cerro Jefe region or from Santa Rita Ridge, two ranges of hills just east of the Canal Zone. Collections from the Canal Zone, including *Fendler 197*, the lectotype, may be varietally distinct from those on the neighboring hills. They have larger, thinner, more rotund leaves, and the pubescence is not so dense overall. *Lycianthes acidochondra* is apparently endemic to central Panama.

Lycianthes acidochondra is similar to *L. guianense* Dun. and *L. pauciflora* (Vahl) Bitt. of the Guyanas and Venezuela; but the fruiting calyx teeth are much stouter, and the fruit is globose.

Williams 570 was cited as one of the two collections upon which Bitter based the name *Solanum acidochondrum*. It is a different species, *L. guianense*. In overall appearance the two species are alike, but the fruit and calyces are different.

When he described *Solanum acidochondru*m, Bitter drew attention to this species as having the largest stone cell concretions of any *Lycianthes* species, reaching 5 mm long. According to his conclusions anent stone cell concretions, *L. acidochondra* has one of the most primitive sorts of fruit in the genus. Other features of the plants are not primitive.

CANAL ZONE: Chagres, *Fendler 197* (GH, MO, US, type collection). Between Chagres Batteries and Fort San Lorenzo, Fort Sherman Military Reservation, high climbing at edge of forest, *Maxon & Valentine 6973* (US). Gamboa, Pipeline Road, 10 mi. N of Gamboa Bridge, *Stern & Chambers 21* (US). COCLÉ: Cerro Gatal Caracoral, 2,700–3,200 ft, *Dwyer & Correa 8994* (MO). COLÓN: Santa Rita Ridge, *Croat 13848* (MO); *D'Arcy & D'Arcy 6165* (MO); *Dwyer 8558* (MO). Santa Rita Ridge, 4–5.5 mi. E of Transisthmian Highway, advanced secondary forest, *Lewis et al. 5261* (MO). PANAMÁ: Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 459* (MO, PMA). Cerro Jefe, *D'Arcy et al. 3965* (MO). Hillside into Finca del Indio, Cerro Jefe, *D'Arcy 5228* (MO). Plentiful in cafetal, Finca del Indio, Cerro Jefe, *D'Arcy 5236* (MO). Cerro Jefe in "*Clusia*" forest, 2,700–3,000 ft, *Tyson et al. 3310* (MO). Cerro Azul to Cerro Jefe, *Tyson et al. 4334* (FSU, MO).

2. **Lycianthes amatitlanensis** (Coult. & Donn. Sm.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 441–2. 1919 [1920].

Solanum amatitlanense Coult. & Donn. Sm., Bot. Gaz. (Crawfordsville) 37: 420. 1904 (Enum. Pl. Guatemala 4: 110. 1895, nomen nudum). SYNTYPES: Guatemala, *Türckheim 11153* (US), *8488* (C, NY, US), *7753* (NY, US); *Donnell Smith 1457* (GH).
Lycianthes ulei Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 437–8. 1919 [1920]. TYPE: Brazil, *Ule 9764* (NY).
L. ulei subsp. *dolichodonta* Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 437–8. 1919 [1920]. TYPE: Ecuador, *Eggers 14409* (A).

Herb or woody *subshrub* to 75 cm tall; stems flexuous, strigose with spreading, coarse, stramineous simple hairs, 1–3 mm long. *Leaves* lanceolate to elliptical, conspicuously oblique, mostly 12–18 cm long, apically acuminate, basally narrowed and rounded, strigose pubescent, especially along the veins beneath, veins 10–15 on each side of the midvein, parallel and arching slightly to the margins; petioles short, to ca. 10 mm long; minor leaves rotund, to 20 mm long, sparingly pubescent on the upper surface. *Inflorescences* axillary, solitary or a fascicle of 2–3 flowers; pedicels 15 mm long, slender, strigose. *Flowers* small, calyx strigose, 1–2 mm long plus the 10 filiform, 3 mm long teeth, enlarging in fruit; corolla (Honduras, *Yuncker 4625*, MO) 5 mm long, yellowish white; stamens equal, the anthers with a fine point, 4 mm long; the androecium and gynoecium not seen. *Fruit* red, juicy, 10 mm long, the calyx becoming 4 mm long and the filiform teeth 4–5 mm long.

This species is quite unlike any other Panamanian species of *Lycianthes* with its very small flowers and pubescence of strigose, simple hairs. The oblique, lanceolate leaves and small, rotund minor leaves are also distinctive.

Lycianthes amatitlanensis is reported from Honduras and Guatemala to Peru and Amazonian Brazil. *Lycianthes storkii* Mort. & Standl. from Costa Rica may be a glabrate race of this species, while *L. chrysothrix* Bitt. from Peru differs mainly in its greater pubescence and slightly larger flowers. *Lycianthes biflora* (Lour.) Bitt., a species widespread in southeast Asia, differs very little from *L. amatitlanense*. Its subsp. *yunnanensis* Bitt. is especially close to *L. amatitlanense*, but it differs in its less pubescent leaves and slightly larger calyx cup.

Lycianthes amatitlanense is a lowland species.

DARIÉN: Cabecero del Río Pirre, *Bristan 1320* (MO, WIS). Río Uruceca, *Bristan 1438* (MO, WIS). Bank above Río Paja, *Stern et al. 599* (GH, US). SAN BLAS: Forest SE of Puerto Obaldía, *Croat 15766, 16792* (both MO).

3. **Lycianthes beckneriana** D'Arcy.[13] TYPE: Panama, *Woodson & Schery 446* (MO).

Tree 5 m tall; twigs drying strongly angled or furrowed, lightly pubescent with short, several-celled, simple hairs. *Leaves* elliptical, apically acuminate, basally obtuse, slightly upfolded from the midvein, pubescent above and beneath

[13] *Lycianthes beckneriana* D'Arcy, sp. nov. Abor, pilis simplicibus parvis sparsim vestita, calyce florenti 1.5–2 mm profunda, dentibus decimis 1.5 mm longis gerenti, statu fructu 6 mm profunda (longa), dentibus 4 mm longis, corolla purpurea, 12 mm longa, area interplicata minute pubescenti, antheris 5 mm longis pyramidalibus.

with weak, simple, white hairs, veins ca. 5 on each side of the midvein; petioles ca. 2 cm long, pubescent; minor leaves wanting. *Inflorescence* solitary or a several-flowered axillary fascicle on a short, stout peduncle, 5 mm long, with a prominent cicatrix; pedicels 20 mm long, puberulent, very slender but broadening slightly upwards, slightly larger in fruit. *Flowers* with the calyx cup 1.5–2 mm long, pubescent mostly at the sides of the teeth, the teeth slender, 1.5 mm long; corolla 12 mm long, glabrate outside with minute hairs on the surface of the interplicae, campanulate, lobed ⅓ the way down; filaments 2 mm long, glabrous, the anthers 5 mm long, apparently free, cordate basally, pyramidal in shape. *Fruit* (?immature) depressed-globose, 10 mm across, the calyx cup enlarging to 6 mm across, and the teeth stouter and 4 mm long.

The material now available of this species does not permit more exact examination of androecium and gynoecium. In the one flower opened by a previous worker (US), there are only two anthers, and these are somewhat damaged. The style is gone.

Lycianthes beckneriana is distinctive in its simple, sparse hairs and the large corolla in a very small calyx. It is known only from the Chiriquí mountains. Similar to *L. storkii* Mort. & Standl., it may represent a Panamanian variant of that species. It is named for John Beckner, St. Petersburg, Florida.

CHIRIQUÍ: Rain forest, Bajo Chorro, Boquete District, 6000 ft, *Davidson 403* (MO). Potrero Muleto to summit, Volcan de Chiriquí, 3,500–4,000 m, tree 5 m, *Woodson & Schery 446* (MO, holotype; GH, US, isotypes).

4. **Lycianthes escuintlensis** (Coult.) D'Arcy, Phytologia 25: 116. 1973.—FIG. 12.

Brachistus escuintlensis Coult., Bot. Gaz. (Crawfordsville) 16: 144. 1891. TYPE: Guatemala, *Donnell Smith 2267* (US, lectotype; F, G, GH, isolectotypes).
Solanum mitratum Greenm. *in* Donn. Sm., Bot. Gaz. (Crawfordsville) 37: 211. 1904. TYPE: Costa Rica, *Donnell Smith 6673* (GH, lectotype; US, isolectotype).
Lycianthes mitratum (Greenm.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 500–501. 1919 [1920].
L. anomala Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 515. 1919 [1920]. SYNTYPE: *Bourgeau 2536* (K).
L. heteroclita subsp. *coalescens* Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 496. 1919 [1920]. TYPE: Guatemala, *Türckheim 11813* (US, lectotype).
Bassovia escuintlensis (Coult.) Standl., Contr. U. S. Natl. Herb. 23: 1304. 1924.
Solanum escuintlense (Coult.) Hunz., Kurtziana 5: 166. 1969.

Herb, shrub or *tree* to 7 m tall; twigs fine-puberulent with minute, weak, simple hairs. *Leaves* to 20 cm long, mostly elliptic, long-acuminate apically, basally acute or acuminate, membranaceous, darker above and obscurely pubescent with minute, ?glandular, simple hairs, beneath glabrous on the lamina, the veins fine pubescent, ca. 5 on each side; petiole short, to 2 cm long; minor leaves sometimes present on terminal portions of the stem. *Inflorescence* mostly solitary, sometimes a few-flowered fascicle; pedicels 2–2.5 cm long, straight, obscurely fine puberulent with simple hairs even smaller than those of the twigs, not altering much in fruit. *Flowers* with the calyx about as broad as deep, 3–4 mm deep, edentate, prominently 5- or 10-ribbed, the ribs drying dark and continuing into the sleeve, often with a whitish appearance due to minute chalky

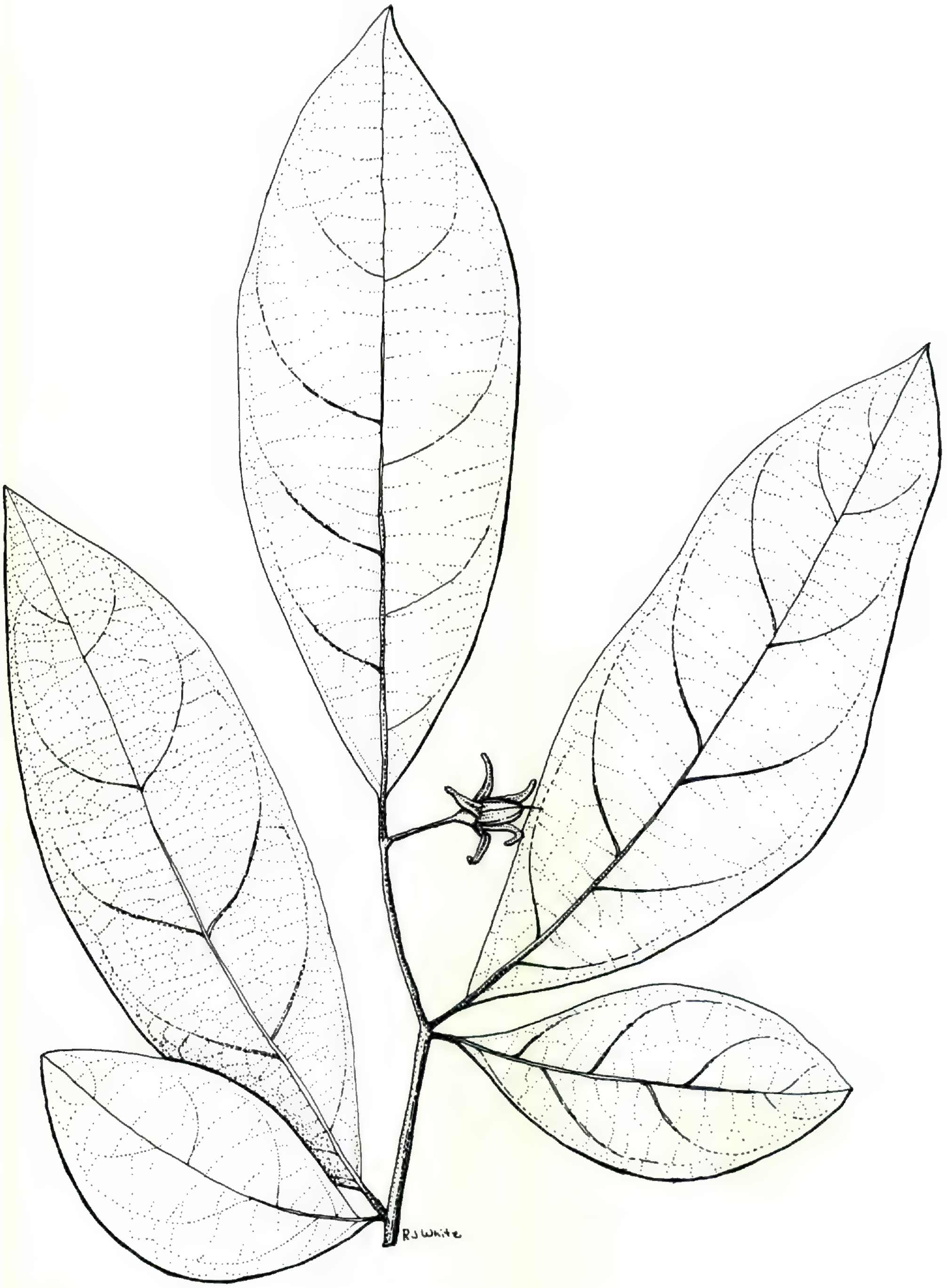

FIGURE 12. *Lycianthes escuintlensis* (Coult.) D'Arcy, branch with flower ($\times$ 3/5). [After *Lewis et al. 2062* (MO).]

trichomes; corolla blue, mauve, or white, ca. 13 mm long, lobed about ⅓ the way down, the interplicae slightly thickened and often whitish-glaucous with minute white trichomes outside, glabrous within; stamens equal, subsessile, connate, 6–9 mm long, forming an ellipsoidal column 5 mm across; style exserted ca. 3 mm, the stigma capitate. *Fruit* a hard berry tightly packed with seeds, ripening red or orange, depressed-globose, often with an apical sulcus; the calyx not accrescent, not applied to the berry.

This species is similar to *L. synanthera*, but it differs in its usually prominently-ribbed calyx, the usual presence of minute whitish trichomes on calyx and corolla, and in the non-barbellate vein axils of the leaf undersides. Specimens in young fruit may be difficult to distinguish from *Witheringia* species. This is perhaps the only species of *Lycianthes* which regularly attains the stature of a tree, and one of the few which does not regularly grow as a climber or vine. *Lycianthes escuintlensis* ranges from Guatemala to Panama, where it occurs principally as a lowland species.

There is a wide range of size in the flowers and in the appearance of the calyx, and more than one species may be present. Most Panamanian material has strongly ribbed calyces with no evidence of lateral teeth, and the anthers are less than 7.5 mm long. Several, but not all, collections from Bocas del Toro have completely obscure calyx ribs, anthers ca. 9 mm long, and calyx ribs that are completely obscure. The type collections of *Lycianthus escuintlensis*, *L. mitratum*, and *L. anomalum* have calyces with almost obscure ribs, but the anthers are about 8 mm long; they are quite similar. These and the Bocas del Toro collections just mentioned have larger than usual calyces (5–6 mm long) with one or more small umbos or teeth which are easily missed on superficial examination. A further variant is found in the material from Darién; the flowers are white, the calyx ribs are not prominent, and the flowers are small with the anthers 5 mm long and the corolla 7 mm long. These variants probably warrant formal recognition at some level.

BOCAS DEL TORO: Lincoln Creek, Changuinola Valley, *Dunlap 574* (US). Río Changuinola near Changuinola, *Dwyer 4620* (MO). Banks of river and adjacent rain forest, 10–15 mi. inland from mouth of Changuinola River, *Lewis et al. 978* (BIRM, F, MO). Rain forest, Chiriquicito to 5 mi. along Río Guarumo, *Lewis et al. 2025, 2062* (MO). Water Valley, *von Wedel 959* (MO, US). Near Chiriquí Lagoon, *von Wedel 1110, 1320* (both MO), *1387* (US), *2467* (MO, US). Near Nievecita, 0–50 m, *Woodson et al. 1814* (GH, MO, NA, NY). CANAL ZONE: Sunny edge of forest, railroad relocation between Gorgona and Gatún, 10–50 m, *Pittier 2281* (US). CHIRIQUÍ: Cerro Horqueta, *Blum & Dwyer 2596* (FSU, GH). Trail to lower edge of cloud forest, NW of Boquete, Cerro Horqueta, 500–5,800 ft, *Dwyer et al. 451* (MO). COCLÉ: Near El Valle, 600–1,000 m, *Allen 1209* (GH, MO, NY, US). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12053* (MO, WIS). El Valle de Anton at foot of Cerro Pilón, 2,000 ft, *Dwyer & Correa 8018* (MO). El Valle, *Ebinger 962* (MO, US). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 585* (GH, MO, NY). El Valle de Anton and vicinity 500–700 m, *Seibert 462* (GH, MO, NY). Near Bajo Mona and Quebrada Chiquero, 1,500 m, *Woodson & Schery 555* (MO). DARIÉN: Edge of Río Peresenico near Río Pirre, *D'Arcy 5529* (MO). Río Pirre near crossing of trail from El Real to Tucuti, 20 mi. W of El Real, *Duke 5189* (MO). Along Pan-Am Highway between Pucro and Río Punusa, *Duke 5398* (GH, MO). Loma Cuasi behind Manene, *Duke 13614* (MO, US, WIS). Between Río Perecenico and Rancho Frío, 500–2,500 ft, seasonal deciduous forest, *Duke & Elias 13866* (C, MO, NY, P). Río Sabana above Santa Fé, *Duke 14113* (MO). Tumaganti, 300 m, *Duke 14167* (ADW, MO, MPU). Premontane rain forest ca. 2 mi. E of

Tres Bocas along the shortest headwater of Río Cuasi, *Kirkbride & Duke 1153, 1157, 1208* (all MO). Tres Bocas on the Río Cuasi, "Toga de monte," "imua" (Choco) used as a narcotic and pain killer, sometimes also used to improve tired eyes, *Kirkbride & Duke 1363* (MO). Between Paya and Boca de Paya, Río Paya, *Stern et al. 434A* (MO). PANAMÁ: Forests along headwaters of Río Corso off Río Pacora, 500 m, *Duke 11906* (MO, OS). Tributary of Río Chagres 5 mi. SW of Cerro Brewster, 1,000 ft, *Lewis et al. 3476* (MO).

5. **Lycianthes guianense** (Dun.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 341. 1919 [1920].—FIG. 13.

Solanum guianense Dun. *in* DC. Prodr. 13(1): 166. 1852. TYPE: Not designated.
Lycianthes pseudolycioides (Chod. & Hassl.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 352–354. 1919 [1920].
Solanum pseudolycioides Chod. & Hassl., Bull. Herb. Boiss., sér. 2. 4: 84. 1904, non Rusby, Bull. Torrey Bot. Club 26: 193. 1899. TYPE: Paraguay, *Hassler 4912* (GH, K, MO).
S. *caucaense* var. *glabrescens* Mort., Contr. U. S. Natl. Herb. 29(1): 58. 1944. TYPE: Colombia, *Archer 2132* (US).
S. *australe* Morton, Contr. U. S. Natl. Herb. 29(1): 62. 1944. TYPE: Paraguay, *Fiebrig 5692* (US).

Vine or *shrub* to 2 m tall; twigs fine-puberulent to tomentose with stellate or dendritic hairs, soon glabrescent. *Leaves* elliptic, to 12 cm long, apically obtuse or acuminate, basally rounded, obtuse or narrowed, somewhat upfolded from the midrib, membranaceous, glabrate on both sides except for a few scattered hairs on the lamina and veins; veins ca. 4 on each side of the midvein; petioles mostly 1–2 cm long; minor leaves mostly wanting. *Inflorescence* solitary or a few-flowered fascicle; pedicels slender, sometimes drying reddish brown, to 12 mm long, glabrate, sometimes with one or 2 normal-appearing stellae present, thicker but not much longer in fruit. *Flowers* with the calyx cup 3–4 mm deep with 10 reflexed, slender teeth in 2 similar series, the longer ca. 7 mm long, the shorter ca. 4 mm long, glabrous except for an occasional normal-appearing hair on the surface and frequently 1 or 2 on the tips of the teeth; corolla white, 14 mm long, the interplicae thickened, glabrous except for a tuft of hairs at the tips of the lobes, only shallowly lobed; stamens unequal, the anther of one surpassing the others by its full length, the other anthers ca. 4 mm long, glabrous; style exceeding all anthers, the stigma ellipsoidal, lateral. *Fruits* pyriform, drying ovoid, red, 15–20 mm across, juicy; fruiting calyx 10–14 mm across, glabrous, the teeth recurved, to 8 mm long, slender or sometimes stout near the base.

Dunal in the original protologue to this species did not clearly designate a type, citing material without flowers labelled S. *glandulosum* in "herb. Banks" (BM) which he had seen in 1819, and also material, undesignated, in "herb. DC" (G-DC) and "herb. Mus. Paris" (P). In Paris is a specimen which appears to be a match for the specimen to be seen on the microfiche of the de Candolle *Prodromus* (IDC 2075 II 6) and which is labelled, "Muséum de Paris 1825." This specimen (the one in Paris) is labelled, "Cayenne, Martin" and is annotated by Bitter himself. Bitter, when he transferred Dunal's *Solanum* species to *Lycianthes* included in his citation a specimen "Cayenne, Martin, ex mus. hort. Paris 1819, hb. Berol," and he discussed comparing it with pieces of the "Dunal'schen Originals" sent him by C. de Candolle of Geneva (G). There is a strong likelihood that the three specimens at Paris, Geneva, and Berlin, the last

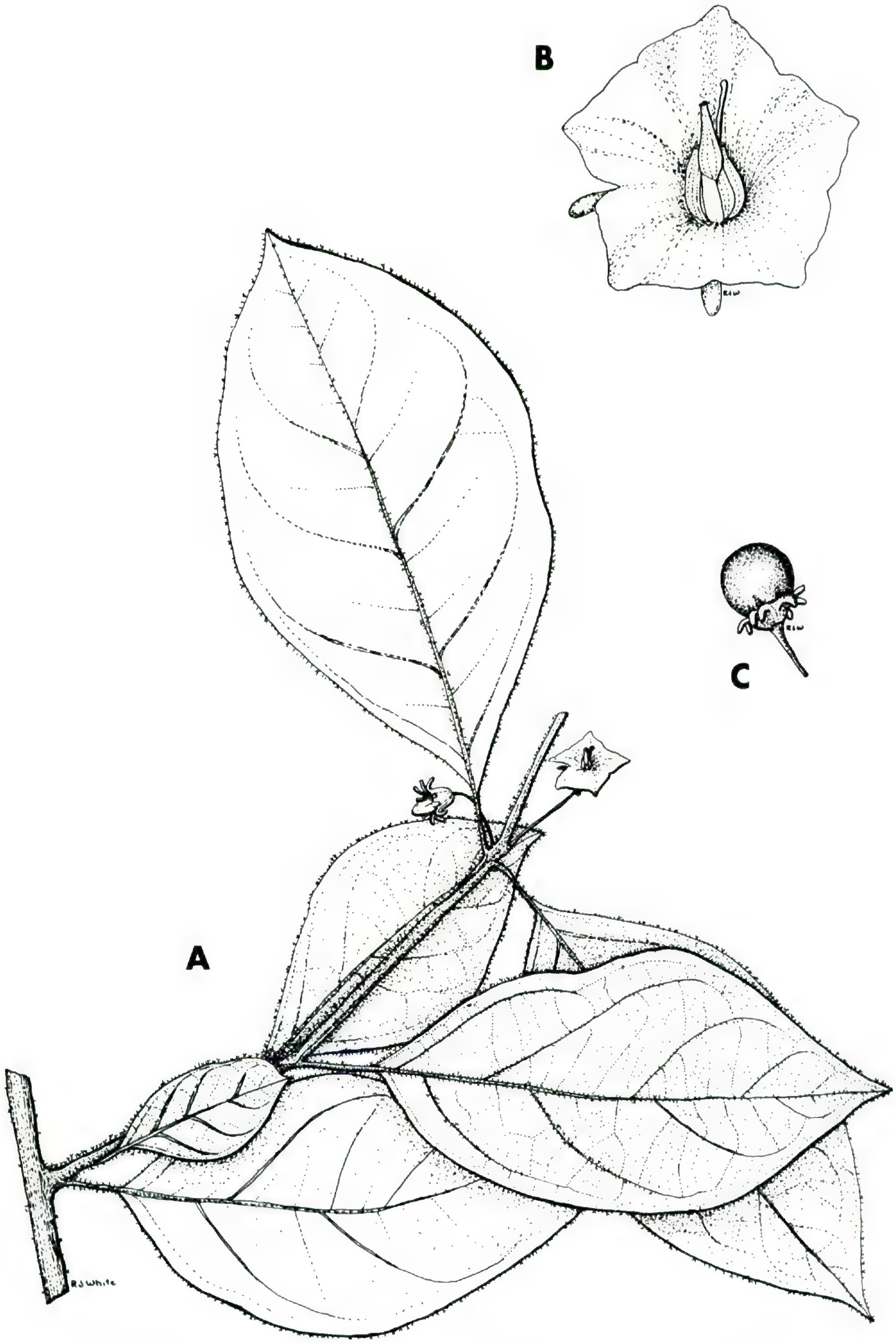

FIGURE 13. *Lycianthes guianensis* (Dun.) Bitt.—A. Flowering branch (× 3/5). [After *D'Arcy 5534* (MO).]—B. Flower (× 2 2/5).—C. Fruit (× 1½). [After photo of *D'Arcy 5534*.]

now destroyed, were from the same collection, and they should be considered authentic material. The Paris specimen is a good match for the Panamanian plants treated here.

Lycianthes guianense is distinguished by its glabrate leaves, glabrate calyx, and unequal anthers. The calyx teeth often dry yellow.

Plants with globose fruits may be taxonomically distinct from those with pyriforme fruits.

This species ranges from Paraguay through Peru, Colombia, and at least as far north as Panama. In Panama, most collections are from middle elevations in Coclé Province but it does range down to sea level.

CANAL ZONE: Pipeline Road, *Gentry 1449* (MO). COCLÉ: Near N rim of El Valle, 600–1,000 m, *Allen 1805* (US). El Valle floor, 600 m, *Allen 3568* (F, GH, MO, NY, US). Hills NE of El Valle de Antón, 2,000 ft, disturbed forest edges, *Lewis et al. 1709* (MO). Bismark above Penonomé, *Williams 570* (US). DARIÉN: Río Pirre below Río Peresenico, *D'Arcy 5534* (MO). Village of Mannene, *Kirkbride & Bristan 1576* (MO). Above Paca near Cana, *Williams 743* (NY). PANAMÁ: Cerro Campana, 2,300 ft, *Blum & Miller 2298* (MO, SCZ). SAN BLAS: Forest above beach E of Puerto Obaldía, *Croat 16921* (MO). VERAGUAS: Above Santa Fé on slopes of Cerro Tute below Agricultural School, 1000–2000 m, *Gentry 6229* (MO).

6. **Lycianthes hawkesiana** D'Arcy.[14] TYPE: Panama, *Dunlap 327* (US, holotype; F, isotype).

Shrub, mostly scrambling or scandent to 3.5 m tall; twigs scurfy to cobwebby-pubescent with mostly sessile, slender-radiate stellate hairs, white. *Leaves* ovate or elliptic, sometimes broadly so, to 18 cm long, short-acuminate apically, basally obtuse or rounded, sometimes slightly oblique or dimidiate, glabrescent on the lamina, the veins puberulent above, ca. 5 on each side of the midvein; petioles 2–3 cm long; minor leaves mostly wanting. *Inflorescence* a several-flowered fascicle on a short, peduncle-like base at a node of the stem; pedicels filiform, 10 mm long, glabrate, becoming stouter and 15 mm long in fruit. *Flowers* with the calyx ca. 2 mm deep with a few scattered, persistent stellae, the teeth slender, 3 mm long; corolla 13 mm long, glabrous near the base, pubescent on the upper portion with sessile stellae; stamens unequal, 4 filaments ca. 1 mm long, the fifth 4 mm long, the anthers 4 mm long, the longer stamen with a slightly larger anther, slender and elongate; ovary ellipsoid, glabrous, 2.5 mm long. *Fruit* ?globose, red, 15–20 mm across, the calyx somewhat accrescent, the cup becoming woody and the teeth ultimately at least partially reflexed and stouter but not much longer.

The slender radii of the whitish cobwebby stellae and the long, filiform calyx teeth on the flower buds distinguish this species from other Panamanian taxa. It is closely related to *L. multiflora* Bitt. of Costa Rica, but that species has short calyx teeth in bud. The calyces of mature fruits tend to resemble those of *L.*

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[14] *Lycianthes hawkesiana* D'Arcy, sp. nov. Frutex, plerumque scandens; ramunculis araneosis pilis stellatibus sessilibus vestitis, foliis glabrescentibus, venis supra puberulentibus; calyce paucis pilis stellatis gerenti, dentibus gracilibus in statu fructu lignosis spissescentibus elongatibusque; corolla extus parte basi glabra exclusa subtiliter pubescenti pilis stellatibus sessilibusque; staminibus inaequalibus; bacca crocea.

guianense of Panama and South America, but there are usually a few hairs remaining at the base of the calyx; *L. guianense* usually has none.

This species is most common in the lowlands of Bocas del Toro and in Coclé at middle elevations. *Lycianthes hawkesiana* is dedicated to Professor J. G. Hawkes of Birmingham, a long-time student of the Solanaceae.

BOCAS DEL TORO: Region of Almirante, *Cooper 164* (F, NY, US). Changuinola Valley, *Dunlap 327* (F, US). Lower Changuinola River, *Stork 49* (US). Without locality, *Carleton 80* (US). Lincoln Creek, *Carleton 83* (NY, US). CHIRIQUÍ: Near Gualaca, Cerro Galera Chorcha, 1,000 ft, *Allen 5056* (MO). COCLÉ: Cerro Pilon, 1 km from top, 900 m, *Correa 45* (MO). Below Cerro Pilon, flat forested area, *Croat 13446* (MO). Cloud forest on slopes of Cerro Pilon near El Valle, 700–900 m, *Duke 12076* (MO). Between Cerro Pilon and El Valle, 700–900 m, cloud forest, *Duke & Dwyer 13925* (MO). El Valle, *Dwyer 1949, 4021* (both MO). Mountains above El Valle, *Stimson 5022* (SCZ). COLÓN: Near Guasimo, forested area on Rio Miguel de la Borda, *Croat 9901* (MO).

7. **Lycianthes howardiana** D'Arcy.[15] TYPE: Panama, *Porter et al. 4899* (MO-2006078, holotype).

High climbing *shrub* or *vine*, ?or *tree*, stems puberulent with short, dense intertwined stellate hairs,[4] the radii slender, whitish and intertwined. *Leaves* ovate, to 13 cm long, apically acuminate, basally rounded, slightly dimidiate, the margins slightly revolute, membranaceous, glabrescent above with a few hairs remaining on the major veins; beneath fine tomentose with short-stalked, slender-radiate hairs, the veins 5–8 on each side of the midvein, conspicuous beneath; petioles slender, puberulent, channelled above; minor leaves wanting. *Inflorescences* terminal, becoming axillary on short shoots bearing one leaf, 1–5-flowered, congested; pedicels stout, tomentose, sometimes lanate, 5–6 mm long. *Flowers* with the calyx lanate-tomentose with whitish stellate hairs, the teeth 10 mm long, appearing stout because of the dense tomentum, the sleeve 1–2 mm long, glabrescent, not much altering in fruit; corolla 13 mm long, glabrous at the base and on the ample plicae, the interplicae thickened and mostly densely white pubescent with sessile stellae which bear elongate, flattened radii; androecium and gynoecium not seen. Mature *fruit* a bright orange, juicy berry 20 mm long; seeds much compressed, yellow-orange, 3 mm long, broadly elliptical in outline.

With its stellate pubescence, purplish flowers and tomentose, elongate calyx teeth, this species is quite distinctive in the Panamanian flora. It is known only from Cerro Campana, ca. 50 km SW of Panama City and ca. 10 km from the bay of Panama. The elevation is about 1,000 m.

This species is named for Dr. R. A. Howard, the Arnold Arboretum.

PANAMÁ: Cerro Campana, high climbing, *D'Arcy & Dressler 5505* (MO). Cerro Campana area, 3,000 ft, above Su Lin Motel, dense woodland bordering roadside, *Dwyer & Kirkbride 7866* (MO). Cerro Campana, *Gentry 4933* (MO). Summit of Cerro Campana, rain forest, *Porter et al. 4899* (MO).

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[15] *Lycianthes howardiana* D'Arcy, sp. nov. Frutex scandens vel labrusca in tectum silvae ascendens, foliis supra grabratis infra venis prominentibus pilis parvis radio mediano tenui vestitis; calyce pilis stellatibus araneosis griseis lanato-tomentoso, dentibus glabrescentibus, vix accrecenti, corolla extus, parte basi glabra exclusa, dense subtiliter pubescenti, bacca aurantiaca livida succida 20 mm longa.

8. **Lycianthes hygrophila** Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 402–3. 1919 [1920]. TYPE: Panama, *Pittier 3263* (US-677654, holotype; US, isotype).

Vine, twigs fistulose, scurfy-pubescent with stellate and dendritic hairs. *Leaves* ovate, ca. 8 cm long, apically acuminate, basally rounded or subtruncate, membranaceous, pubescent above with stout simple hairs, beneath glabrate with scattered minute, simple or pulverulent hairs, veins ca. 4 on each side of the midvein; petioles short or elongate, to 4.5 cm long, glabrescent. *Inflorescence* a solitary flower in the leaf axil; pedicels slender, elongate, 3 cm long, pubescent with dendritic and stellate hairs. *Flowers* with the calyx cup 4 mm deep, pubescent with simple and dendritic hairs, the 10 teeth 4–5 mm long, pubescent with mostly simple hairs; corolla "pale purple," ca. 18 mm long, the margin almost entire, the interplicae thickened, glabrous; stamens (fide Bitter) equal, the filaments 1 mm long, glabrous, somewhat thickened, the anthers broadly lanceolate-ellipsoid, 6 mm long and 2 mm broad at the base, emarginate at each end; ovary ellipsoid, 2 mm long, 1.3 mm broad, glabrous, the apex abruptly attenuate into a straight, glabrous style ca. 9 mm long which exceeds the anthers, the stigma subglobose, obtuse. *Fruits* unknown.

This species is known only from the type collection, which now bears only one flower; examination of its interior is inadvisable, thus details of androecium and gynoecium are taken from Bitter's original description.

The nature of the hairs of this species is quite distinctive among the Panamanian species of *Lycianthes*. Those on the leaf uppersides and on the calyx teeth are simple, 1–4-cells-long, but otherwise resembling the stellate and dendritic hairs of the stem and pedicels. Hairs on the leaf undersides are much reduced, the simple ones mostly only 1-cell-long and the radii of the stellate or pulverulent ones only 1-cell-long.

CHIRIQUÍ: Humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2,100–2,268 m, vine, flowers pale purple, *Pittier 3263* (US).

9. **Lycianthes luteynii** D'Arcy.[16] HOLOTYPE: Panama, *Luteyn 836* (MO).

Shrub or *vine*, twigs rusty tomentose with stellate hairs, some with stout stalks. *Leaves* ovate, to 15 cm long, basally rounded, oblique, apically acuminate, membranaceous, veins 3–4 on each side of the midvein, above puberulent with stalked, slender-armed stellae, beneath tomentose and drying lighter; petioles tomentose, ca. 15 mm long, channelled. *Inflorescence* a several-flowered fascicle, the peduncle obsolete but marked by a cicatrix from fallen pedicels, pedicels tomentose, sturdy, 10–15 mm long (fruiting). *Flowers* not seen. *Fruit* (immature) a globose or ovoid berry subtended by the tomentose calyx, the teeth 10 in 2 subequal series protruding only 1–2 mm beyond the tomentose sleeve and perhaps fused with it, the cup ca. 10 mm across.

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[16] *Lycianthes luteynii* D'Arcy, sp. nov. Frutex v. labrusca, caulibus tomentosis pilis stellatibus, foliis supra sparse stellatibus, subtus tomentosis; calyce fructifer tomentosis, dentibus parvis.

This species is known only from the type collection, taken from an upland area of the Chiriquí Mountains now undergoing clearing for cattle pasture. It is similar to *L. howardiana* of Central Panama but the calyx is much shorter, and the indumentum has a quite different appearance. It is named for James Luteyn, Duke University, collector of this and other interesting Panamanian Solanaceae.

CHIRIQUÍ: Upland woods along clearing path, 5.2 mi. NW of El Hato de Volcán on road to Costa Rica, 5500 ft, *Luteyn 836* (MO).

10. **Lycianthes maxonii** Standl., Jour. Washington Acad. Sci. 17: 14. 1927. HOLOTYPE: Panama, Barro Colorado Island, *Maxon et al. 6808* (US).

10a. **Lycianthes maxonii** Standl. var. **maxonii.**

L. maxonii var. *appendiculata* Standl., Jour. Washington Acad. Sci. 17: 15. 1927. HOLOTYPE: *Standley 28040* (US).

Herb or *shrub* to 1.5 m tall, erect, or somewhat spreading; stems slender, twigs puberulent with short, weak hairs; sarmentose. *Leaves* mostly elliptic or oblong, sometimes ovate or obovate, chartaceous, to 15 cm long, apically short acute, basally obtuse or acute, mostly symmetrical, dark green above, mostly glabrous on both sides but sometimes puberulent on the veins, veins 4–6 on each side of the midvein; petioles short, to 5 mm long; minor leaves wanting. *Inflorescence* solitary or a few-flowered fascicle, sometimes on a short peduncle, ca. 2 mm long, with a prominent cicatrix on its dorsal side; pedicels filiform, 15 mm long, glabrate, often drying yellow. *Flowers* with the calyx glabrous, tubular, 2 mm deep, the sides straight, umbonate or with distinct and sometimes elongate teeth, the sleeve ca. 0.75 mm long; corolla blue or purplish, 5–7 mm long, deeply lobed; stamens equal, the filaments glabrous, 1 mm long, the anthers 4–5 mm long, connivent to connate, opening by terminal pores with slightly protracted lips. *Fruits* red, juicy, globose, ovoid, obovoid or ellipsoidal, ca. 5 mm across.

The small blue or purple flowers and red fruits separate this species from other Panamanian species of *Lycianthes*. The chartaceous and often elongate leaves are frequently sufficient for recognition of sterile material. *Lycianthes maxonii* is an understory species of central Panama, mostly found in mature forests. It is also found in cutover forest areas and cafetales, where it sometimes flowers from turoins. There are specimens of this taxon at Chicago (F) from Nicaragua and Costa Rica.

Standley's var. *appendiculata* is based on a specimen with very slender teeth, slightly longer than usual, and a sleeve slightly longer than usual, but this is merely an extreme within the predictable range of variation for the species. *D'Arcy 5507* matches the type of var. *appendiculata*: it was collected a year later but from the same plant as *D'Arcy 3939*, a collection with normal calyces.

CANAL ZONE: 12 S Colón on Río Providencia, *Tyson et Blum 3942* (FSU, MO, SCZ), *3992* (MO); *Tyson et al. 4479* (FSU, MO). Barro Colorado Island, *Aviles 31, 43b* (both MO); *Croat 6307* (DUKE, MO, NY), *6489, 6508, 6624, 8611, 9421* (all MO), *10092* (DUKE, MO), *10979, 11454, 11896* (all MO); *D'Arcy 3939* (ADW, BIRM, C, F, MO, MPU, UCWI), *5507* (MO); *Ebinger 550* (GH, MO); *Hayden 1036* (MO); *Shattuck 277* (F, MO, US), *1015* (MO); *Standley 31326* (US), *31365* (MO), *40880, 41088, 41145* (all US). CHIRIQUÍ: In woods above Nueva Suisa, Volcán District, 6,000 ft, *D'Arcy 5322* (MO, MPU, PMA).

COLÓN: Forest along trail, Río Indio, *Steyermark & Allen 17455* (MO). DARIÉN: Cocalito near Darién-Choco (Colombia) boundary, *Dwyer 3105* (MO). PANAMÁ: 3.5 mi. W of Goofy Lake near Cerro Azul, *Croat 11561* (MO). One plant in recently cleared forest, Cerro Jefe, *D'Arcy et al. 3960* (MO). Summit of Cerro Jefe and forests along road beyond summit, *Hayden 1011* (MO). Rain forest, Chimán, *Lewis et al. 3257* (ADW, BIRM, MO, MPU). Near Arenoso, lower Río Trinidad, 26–50 m, *Seibert 612* (MO). Río Tapia, moist forest, *Standley 28040* (US).

10b. **Lycianthes maxonii** var. **grandidentata** D'Arcy.[17] HOLOTYPE: Panama, *Lewis et al.* 5383 (MO).

Calyx 2–4 mm deep and broader than deep, mostly bearing 5 stout teeth, ca. 1 mm long, the sleeve very short and inconspicuous; corolla ca. 7 mm long, white but sometimes drying with a hint of blue.

This variety may warrant specific recognition, but it is apparently closely related to var. *maxonii*. All collections to date are from Santa Rita Ridge, an area (elevation to 750 m) adjacent to the northeastern portion of the Canal Zone, where var. *maxonii* is plentiful. The calyx is proportionally much shorter and the teeth much stouter than on the material Standley referred to var. *appendiculata*. This variety also bears a close resemblance to material in Paris (P) labelled "*Solanum membranaceum* Wall. = S. *laeve* Dun," which probably originated in the East Indies.

COLÓN: Santa Rita Ridge, 5.5–6 mi. E of Transisthmian Highway, rain forest, *Lewis et al.* 5383 (F, MO, MPU). Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi. from highway, advanced secondary forest, *Porter et al. 4765* (MO, PMA), *4784* (ADW, BIRM, F, MO), both collected on the same day.

11. **Lycianthes porteriana** D'Arcy.[18] TYPE: Panama, *von Wedel 732* (US).

Shrub or *vine*, twigs arachnoid-puberulent with brownish stellate hairs, fistulose. *Leaves* ovate, ca. 15 cm long, basally rounded or obtuse, apically acute or acuminate, membranaceous, veins 3–4 on each side of the midvein, glabrescent and drying slightly darker above, tomentose beneath with stalked, slender-armed stellae; petioles to 10 mm long. *Inflorescence* a several-flowered fascicle, the pedicels slender, ca. 14 mm long, conspicuously pubescent with stalked stellae, the peduncle obsolete but marked by a cicatrix from fallen pedicels. *Flowers* with the calyx tomentose but the tissue clearly visible beneath the pubescence, the cup ca. 5 mm across, shallow, the teeth 10 in 2 similar series, slender, elongate, 4–5 mm long; corolla white (*von Wedel*), 6–7 mm across in bud, finely tomentose, ca. 14 mm long in flower. *Fruit* not seen.

This species is distinctive in its pubescent, slender, and elongate calyx teeth. It differs from *L. howardiana* in its slender calyx teeth and longer, slender pedicels, and from *L. luteynii* which has short, stouter calyx teeth and stout pedicels which, however, have been seen only in fruit.

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[17] *Lycianthes maxonii* var. *grandidentata* D'Arcy var. nov. Differt a varietate typica dentibus crassioribus calycis maji, corolla alba nec purpurea.

[18] *Lycianthes porteriana* D'Arcy, sp. nov. Frutex vel labrusca leviter stellato-tomentosus, pedicellis gracilis elongatis, dentibus calyce gracilis, elongatis distinctus.

Several fragmentary collections from Bocas del Toro seen in various herbaria may be this species.

The species is named for Duncan M. Porter, formerly of the Missouri Botanical Garden.

BOCAS DEL TORO: Water Valley, *von Wedel 732* (US). Without locality, *von Wedel 242* (MO).

12. **Lycianthes synanthera** (Sendt.) Bitt., Abh. Naturwiss. Vereine Bremen 24(2): 499–500. 1919 [1920].

Solanum synantherum Sendt., Flora 29(13): 178 [194]. 1846. TYPE: Guatemala, *Friedrichsthal 1292* (?W, not seen; MO, photo).
Lycianthes chiriquiensis Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 22: 100–101. 1940. TYPE: Panama, Chiriquí, Boquete, 1140 m, *Davidson 623* (F, holotype; US, isotype).

Shrub or *tree* to 10 m tall; sometimes (?hemi-)epiphytic; twigs glabrate with only a few minute, pulverulent hairs near the nodes or none. *Leaves* elliptic, apically long-acuminate, basally acute or obtuse, chartaceous, glabrous above but often drying with a punctate appearance, glabrate beneath and often barbellate in the vein axils, often some scattered hairs along the midvein; petioles 1–2.5 cm long; minor leaves wanting, or when present like the majors and giving the node an opposite-leaved appearance. *Inflorescence* solitary or a few- to many-flowered fascicle; pedicels slender, drying dark, glabrous or with a few minute, degenerate hairs, ca. 18 mm long, not altering much in fruit. Flowers with the calyx cyathiform, glabrous, edentate with little suggestion of teeth, 2–3 mm deep; corolla purplish, 10 mm long, lobed to near the base with narrow, membranous plicae, glabrous except for a few hairs at the tip of the lobes; stamens equal, the anthers 6–7 mm long, united into an ellipsoidal column ca. 3 mm across, glabrous, yellow; style slender, exserted. *Fruits* globose, fleshy, 7 mm across; the calyx becoming a woody peltate disc 5–6 mm across, free from the fruit; seeds 1.5 mm across, discoid with a distinct margin, foveate, yellow.

In many specimens seen, the anthers are firmly connate. But this may not be so in all plants, and further field studies will be necessary to ascertain whether this connation is of specific importance. Bitter and Sendtner both note similarity between this species and *L. heteroclita* (Sendt.) Bitt. and indicate they differ mainly on the connation of the anthers. Bitter nevertheless described varieties of *S. heteroclita* with syngenesious anthers. No type material or photographs of type material of *S. heteroclita* have been seen at this writing, and this name is not used in the present treatment. Many collections labelled as *L. heteroclita* are referred to *L. synanthera*.

This taxon is one of the most frequently collected of all species of *Lycianthes*. It ranges from Mexico to Panama. A species of lower and middle elevations, it is apparently persistent in areas of disturbance.

Lycianthes synanthera is similar to *L. stellata* (Jacq.) Bitt. of the Antilles, but that species has incipient teeth and a shorter sleeve. Specimens in bud may be difficult to distinguish from species of *Witheringia*.

BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper 396* (F, US). CANAL ZONE: Drowned forests of Quebrada Culebra, *Dodge & Allen 17050* (G). Barro Colorado

Island, Wheeler trail, *Croat 10094* (ADW, BIRM, C, F, MO, MPU, PMA, UCWI), *10213*, *11665*, *11899* (all MO). CHIRIQUÍ: Progreso, *Cooper & Slater 298* (A, F, NY, US). COCLÉ: Epiphyte, El Valle, *Blum et al. 2383* (FSU, MO, PMA). Forest behind Club Campestre, 700 m, *Duke 13254* (MO). El Valle, *Dwyer 1841* (GH, MO). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7956* (COL, DUKE, MO, SCZ, UC). Cerro Pilón, 2,700 ft, *Dwyer & Lallathin 8611* (MO), *8615* (MO, NY). Second growth forest, road behind pension at El Valle, *Ebinger 949* (GH, MO, US). Without locality, *Hunter & Allen 585* (G, GH, MO, NY). Hills NE of El Valle de Antón, 2,000 ft, disturbed forest edges, *Lewis et al. 1712* (MO, US). El Valle, *Tyson et al. 3966* (SCZ). COLÓN: Vicinity Giral near bat cave, *Blum & Tyson 516* (MO, SCZ). PANAMÁ: Along highway near top of Cerro Campana, *Croat 12087* (MO). Forests along headwaters of Río Corso, 500 m, *Duke 11925* (MO, OS). Río Pacora just below confluence with Río Corso, *Duke 12005* (MO, WIS). VERAGUAS: Tute, *Dwyer 4281* (MO).

13. **Lycianthes tysoniana** D'Arcy.[19] TYPE: Panama, *Porter et al. 5056* (MO, holotype).

Shrub or sprawling *vine*; stems glabrescent, drying almost black, twigs ferrugineous with mostly short-stalked, long-radiate, stellate and dendritic hairs. *Leaves* coriaceous, to 7 cm long, broadly ovate or elliptic, apically obtuse or short acuminate, basally rounded or obtuse, the margins strongly revolute, glabrescent above with obscure venation and drying black, the veins prominently elevated beneath, tomentose to glabrescent, the lamina glabrous drying yellow-green, veins ca. 2 on each side; petioles short, ca. 10 mm long; minor leaves wanting or equalling the major leaves, the nodes thus appearing opposite-leaved. *Inflorescence* solitary or a few-flowered fascicle; pedicels persistently ferrugineous, 10 mm long, elongating to 20 mm and thickening in fruit. *Flowers* with the calyx cup 4 mm deep, pubescent, with 10 well-spaced teeth 5 mm long; corolla with thickened pubescent interplicae, mature flowers not seen. *Fruit* shiny, bright orange or red, ca. 14 mm across; the calyx scarcely enlarged; seeds large, compressed-discoid, ca. 5 mm long with a thickened margin.

Superficially, the texture of the leaves and young flowers is strongly suggestive of *L. acidochondra*, which grows in the same region. However, the glabrous lamina and usually glabrescent veins on the leaf undersides and the non-accrescent calyx are manifest distinctions.

All collections to date are from Cerro Jefe, an area of seasonal lowland cloud forest of about 750 m elevation.

PANAMÁ: Cerro Jefe, *Dwyer 8085* (MO). Cerro Jefe, 2,900 ft, forest edge and road bank, sprawling shrub, fruit shiny orange, *Dwyer & Gauger 7353* (MO). Advanced secondary cloud forest, Cerro Jefe, *Porter et al. 5056* (MO).

12. LYCOPERSICON

Lycopersicon Mill., Gard. Dict., abr. ed. 1754. TYPE: *L. esculentum* Mill.

Lycomela Heister *ex* Fabr., Enum. Meth. Pl. 194. 1759, not seen; ed. 2. 348. 1787.
Lycopersicum Hill., Veg. Syst. 9: 32. 1765.

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[19] *Lycianthes tysoniana* D'Arcy, sp. nov. Labrusca, vel frutex scandens, caulibus glabrescentibus, foliis supra glabris atrantibus nervis obscuris, subter lutescentibus, nervis prominentibus, glabrescentibus, calyce vix accrescenti.

Amatula Med., Malvan = Fam. 106–108. 1787.
Psolanum Neck., Elem. 2: 60, No. 707. 1790.
Licopersicum Neck., Elem. 2: 61, No. 708. 1790.
Solanum L. sect. *Lycopersicon* von Wettst. *in* Engler & Prantl, Nat. Pflanzenfam. 4(3b): 24. 1891.
Solanopsis Börner, Abh. Naturwiss. Vereine Bremen 21: 282. 1913, pro parte.

Unarmed sprawling ephemeral or perennial *herbs*, glandular or viscid and aromatic; stems soft and weak, in a few species woody near the base, to 1 m long. *Leaves* mostly pinnately lobed or divided, smaller interstitial leaflets often present between the major leaflets or on the petiole, the leaflets sessile or stalked, toothed, lobed or entire, the leaves sometimes (mostly on juveniles) simple and entire; petioles elongate; minor leaves mostly present and conspicuous, sometimes in pairs and appearing stipule-like. *Inflorescences* several, lateral, each a several-flowered raceme or panicle, the peduncle mostly unbranched or once branched near the base; pedicels slender, articulating above the base. *Flowers* 5-merous or mostly 6–9-merous in cultivated species; calyx divided almost to the base, the lobes lanceolate, densely pubescent but glabrescent, accrescent and the lobes reflexed in fruit; corolla yellow, greenish or white, rotate-stellate with a short tube and lanceolate lobes which approximate the calyx lobes in length; stamens equal, erect, the filaments short, the anthers narrowly oblong or tapering to a point, coherent into a tube by intermeshed lateral hairs and densely pubescent within the tube, each anther with a sterile, conical, terminal appendage, dehiscent introrsely by longitudinal lateral slits; ovary 2-loculed, the ovules on large axile placentae which often (in cultivated species) ramify and divide the fruit into several or many locules, the stigma included or exserted from the antheridial column. *Fruit* a juicy berry, glabrous or pubescent, variously colored or white, mostly edible; seeds laterally much compressed, glabrous or pilose, the embryo large, coiled around the periphery of the seed.

A genus of six species and several varieties centered in the coastal region of western South America from Colombia to northern Chile, with two species in the Galapagos Islands. One species, the cultivated tomato, is an important food crop in many countries and it is naturalised in a number of subtropical and tropical areas.

Lycopersicon is a close relative of subg. *Potatoe* of *Solanum*, but despite the affinity of *Lycopersicon* and this section of *Solanum*, there are some important differences. The yellow flower color, appendaged coherent anthers which dehisce longitudinally and the alkaloid chemistry are different in *Lycopersicon*. Tomatidin alkaloids of *Lycopersicon* are replaced by solanine compounds in the genus *Solanum*. There is ecological distinction too, for tomatoes are essentially lowland plants but occur in mountainous areas where there is no frost, while potatoes are upper elevation plants which frequently grow in areas of prolonged frost. There appears to be a distinct evolutionary gap between the species now placed in *Lycopersicon* and those considered to belong to *Solanum*, and the gap is of generic magnitude. When such gaps are identified and documented within *Solanum*, it may be desirable to extract other genera from that large and diverse genus.

The genus takes its name (*lyco* = wolf; *persicon* = peach) from a fancied

similarity to a plant named *Lycopersicon* by the early Greek, Galen, ca. 130–200 A.D. Plants of this genus were unknown to the early Greeks. Today it is commonly known in English as "tomato." In Spanish, the plant is a "tomatero" and the fruit a "tomate."

Useful references:

Luckwill, L. C. The genus *Lycopersicon*. Aberdeen Univ. Stud. 120. 1943.

Muller, C. H. A revision of the genus *Lycopersicon*. U. S. D. A. Misc. Pub. 382. 1940.

———. The taxonomy and distribution of the genus *Lycopersicon*. Natl. Hort. Mag. 19: 157–160. 1940.

1. **Lycopersicon esculentum** Mill., Gard. Dict., ed. 8. 1768. TYPE: (not seen).[20]

Sprawling ephemeral *herbs* to 1 m long, viscid-pubescent and strongly aromatic. *Leaves* to 25 cm long and 20 cm broad, broadly ovate, mostly pinnatisect, the lobes on petiolules often toothed, alternating with minor interstitial leaflets; petioles 2–5 cm long; minor leaves often large and conspicuous, often in pairs. *Inflorescence* lateral, few-to-several-flowered, the peduncles to 7 cm long, pedicels articulating in the lower half; flowers (5–)6–9-merous. *Flowers* with the calyx accrescent and reflexed in fruit; corolla yellow, 6–9 mm long; filament flattened dorsally, anthers 11–14 mm long, coherent into a stout tube; ovary with some minute, erect, simple hairs, the stigma included. *Fruit* a large, red or yellow, juicy berry to several cm in diameter, the placenta fleshy and much ramified. *Seeds* 2–3 mm in diameter, discoid, compressed and thick-winged, yellow, the surface appearing smooth but if cleaned then evidently pilose.

This species is a traditional cultivated plant in all parts of Panama. Dooryard culture provides a great variety of fruit appearance, and in smaller towns these fruits find their way into markets. A substantial acreage of tomatoes in the Natá-Penonomé area of Coclé Province under the direction of the Nestlé Company is devoted to a variety producing a very uniform, attractive ovoid fruit. This crop is manufactured and also sold fresh in major markets throughout Panama. Specimens seen in herbaria are probably all from plants spontaneous from cultivated fruits. They may not be long persistent in Panama.

COCLÉ: 10 mi. E of Natá at Río Grande, common cultivated tomato, *Tyson 5225* (MO). LOS SANTOS: Ca. 6 mi. S of Las Tablas, in weedy area, *D'Arcy & Croat 4183* (MO). PANAMÁ: Panama City, weed behind auto shop beside Ancón Hill, *D'Arcy 3924* (MO).

13. MARKEA

Markea L.-Cl. Rich., Act. Soc. Hist. Nat. Paris 107. 1792. TYPE: *M. coccinea* L.-Cl. Rich.

Lamarckea Pers., Syn. 1: 218. 1805. TYPE: Based on *Markea coccinea* L.-Cl. Rich.
Marckea A. Rich., Dict. Class. 10: 168. 1826. TYPE: Based on *Markea coccinea* L.-Cl. Rich.

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[20] For a list of synonyms, see Muller (1940*a*). None of these names has been used for Panamanian material.

Dyssochroma Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 250. 1849. TYPE: *Solandra viridiflora* Sims (= *Markea viridiflora* (Sims) Ducke).
Ectozoma Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 191. 1849. TYPE: *E. pavonii* (Miers) D'Arcy.[21]
Merinthopodium Donn. Sm., Bot. Gaz. (Crawfordsville) 33: 11. 1897. TYPE: *Markea neurantha* Hemsley.

Unarmed *shrubs* or *vines*, mostly *hemi-epiphytes*; stems mostly slender with a large, often fistulose pith, the twigs often an expanded cicatrix from fallen leaves and inflorescences. *Leaves* simple, entire, mostly clustered at the ends of the twigs; minor leaves wanting. *Inflorescences* appearing terminal at the ends of twigs, solitary or variously paniculate, racemose or corymbose, sometimes pendant below the leaves, peduncles short and stout in some species and in others very long and slender; pedicels mostly either short or very long. *Flowers* inconspicuous or showy, calyx 5–35 mm long, fleshy and globose or tubular, split into 5 short or long lobes, glabrous; corolla valvate and mostly pointed in bud, 7–100 mm long, mostly campanulate, actinomorphic, the tube short and the limb (cup) well-developed, angled near the base and sometimes tubular, the lobes short, recurved or not; stamens 5, equal, the filaments straight, inserted near the base of the limb, the anthers elongate, rarely linear, 4-loculed, dehiscing longitudinally, sometimes apiculate, exserted or not; ovary superior to partly inferior, sometimes short stipitate with a nectariferous disc partially or wholly represented near the base, 2-loculed, the ovules many. *Fruit* a conical or obovoid leathery berry which approximates the length of the calyx lobes; seeds somewhat flattened, often bent; embryo curved or almost straight.

As now constituted, *Markea* embraces about 20 species of questionable affinity. The generic limits and possible relationships between species now placed in *Juanulloa*, *Solandra*, and *Markea* are not well understood. Comparative studies of these three genera plus such poorly known groups formerly known as *Ectozoma*, *Sarcophysa*, etc., are desirable, but collections of some of these are unique, and material is not sufficient to permit dissections or other technical operations. The Panamanian species of *Markea* are here considered to fall into three sections[22] which may at some time be segregated as distinct genera. Section *Megalandra* is in some respects intermediate between sect. *Markea* and the genus *Solandra*—

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[21] *Markea pavonii* (Miers) D'Arcy, comb. nov. Basionym: *Ectozoma pavonii* Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 191. 1849.

[22] The infrageneric taxa of *Markea* are distinguished as follows:

a. Calyx fleshy, splitting a short way in flower, further in fruit; ovary partly inferior; leaves broad, coriaceous, drying yellowish or greyish, the undersides glandular punctate, and venation obscure or impressed above ..... sect. *Megalandra* (Dun.) D'Arcy
aa. Calyx mostly not very fleshy and splitting more than halfway; ovary superior; leaves not punctate beneath, venation not impressed above, mostly not coriaceous.
  b. Flowers less than 2 cm long, anthers ovoid, apiculate; calyx parted before egress of corolla, not splitting later (except perhaps in fruit) ..... sect. *Granatense* D'Arcy
  bb. Flowers longer than 2 cm, anthers elongate; calyx splitting partway down.
    c. Inflorescence elongate, calyx lobes oblong with acuminate, linear tips; anthers included ..... sect. *Markea* (including sect. *Merinthopodium* (Donn. Sm.) Cuatr.)
    cc. Inflorescence not elongate, calyx lobes acuminate; anthers exserted ..... sect. *Dyssochroma* (Miers) Cuatr. (not in Panama)

the anthers are relatively short, the corolla is imbricate in bud, the leaves are coriaceous, and there is a strong suggestion of perigyny. Several species described in *Solandra* are congeneric with *Markea* sect. *Megalandra*, but the calyx structure, punctate leaves, degree of perigyny, anther shape and corolla size distinguish this section from *Solandra*.

Most species of *Markea* are myrmecodomatial, the ants often innocuous but sometimes hazardous to botanists or others intruding on their precincts. The flowers of several species of *Markea* open nocturnally, *e.g. M. dressleri*, and in the daytime fully opened flowers are to be found only on the forest floor. These flowers are probably visited by bats: bat pollination of *Markea* species with like flowers has been documented (Vogel, S. Fledermausblumen in Sudamerika. Oesterreich. Bot. Zeitschr. 104: 491–530. 1958).

The genus takes its name from Jean Antoine Pierre Monnet de Lamarck, 1744–1829, a noted French biologist. The apparent orthographic corrections by A. Richard to *Marckea* and by Persoon to *Lamarckea* are not in the interest of nomenclatural stability.

a. Corollas less than 15 mm long (C. sect. *Granatense*) ..... 5. *M. ulei*
aa. Corolla more than 30 mm long.
  b. Leaves coriaceous, glandular punctate beneath (under a lens), the margins revolute, peduncles and pedicels short (B. sect. *Megalandra*).
    c. Calyx less than 20 mm long ..... 4. *M. megalandra*
    cc. Calyx more than 30 mm long ..... 3. *M. crosbiana*
  bb. Leaves membranaceous, not punctate beneath; inflorescence (peduncle plus pedicel) elongate, more than 5 cm long (A. sect. *Markea*).
    d. Leaf venation strongly ascending, mostly arising from the basal half of the leaf, leaves very broad; corolla 8 cm long; calyx 4 cm long including the slender terminal appendage ..... 1. *M. dressleri*
    dd. Leaf venation ascending at ca. 45°, not arising mostly from the basal portion of the leaf, leaves more than 2 times as long as broad; corolla 4–5 cm long, calyx ca. 1.5 cm long without an elongate terminal appendage ..... 2. *M. neurantha*

A. Section **Markea.**

Sect. *Merinthopodium* (Donn. Sm.) Cuatrec., Fedde Repert. 61: 77. 1958. TYPE: *Markea neurantha* Hemsl.

1. **Markea dressleri** D'Arcy.[23] TYPE: Panama, *Dressler* 3773 (MO-1996691, holotype; DUKE, K, MPU, PMA, isotypes).—FIG. 14.

Shrub, epiphytic in trees, branches drying with ribbed and flaking bark, twigs chocolate brown, splitting and ribbed longitudinally with large scattered lenticels. *Leaves* clustered at the ends of twigs or on short shoots, ovate to broadly elliptic, 6–20 cm long and 4–15 cm broad, apically short acuminate and basally acuminate to cuneate, membranaceous, glabrous except for a very few small simple hairs on the midvein beneath, veins 3–5 on each side, strongly ascending, prominent

[23] *Markea dressleri* D'Arcy, sp. nov. Labursca vel frutex altus scandens, *Markea neurantha* simile, differt venis foliorum valde ascendentibus, plerumque dimidio inferiore exorientibus, foliis latissimis; corolla 8 cm longa, calyce caudis gracilibus incluso 4 cm longo. Nomen Roberti L. Dressleri botanici amicique botanicorum in annuis panamae incola designatur ad hanc *Markeam*.

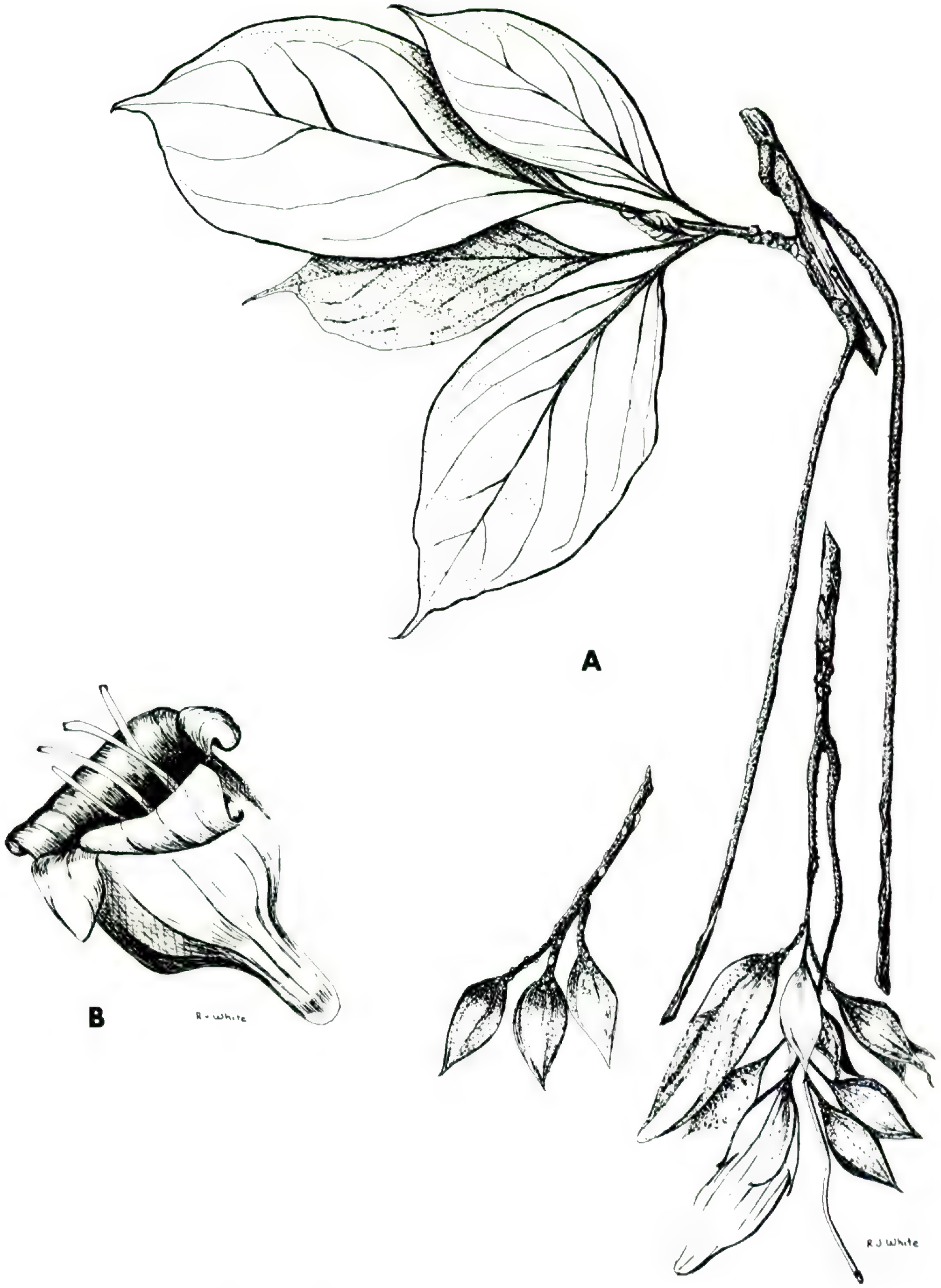

FIGURE 14. *Markea dressleri* D'Arcy.—A. Flowering branch (× ½). [After *Dressler 3773* (DUKE).]—B. Corolla with emergent filaments (× ⅗). [After photo of *D'Arcy et al. 3951*.]

beneath; petioles 2–5 cm long, channeled above and pubescent on other surfaces. *Flowers* clustered at the end of a long, slender, sometimes branched peduncle, to 50 cm, the peduncle roughened with minute tubercules and expanded into a stout elongate terminal length of scar tissue; pedicels slender, expanding upwards, ca. 1.5 cm long, puberulent, sometimes warty; calyces very strongly angled, 2.5–4 cm long, split nearly to the base at anthesis, the lobes deltoid, elongate, puberulent with minute hairs; corolla green, minutely puberulent outside, madder purple inside with a narrow margin of green at the lobes, 7–8 cm long, campanulate, apparently opening nocturnally; anthers elongate, ca. 12 mm long and 2 mm wide, apiculate, the theca opening through 90° and becoming flat, exserted; style white, elongate, 6–8 cm beyond the calyx, persistent on the fruit for a time, stigma globose-ovoid, small. *Fruit* (immature) ovoid-conical, not exceeding the calyx, with a conspicuous terminal scar.

Markea dressleri is similar to *M. neurantha*, differing in the very broad leaves with strongly ascending veins and in the larger flower size. One specimen with flower dimensions like this from Costa Rica (*Austin Smith H91* (MO)) may be the same species.

This species is apparently a night bloomer as corollas are found in abundance on the forest floor, but no open flowers are to be seen on the plants in the daytime. The region where it occurs is at about 1,000 m elevation and is subject to a seasonal rainfall pattern. The collections were made from about 7 m high in a tree in an undisturbed forest area along the bank of the upper Río Casicadas on Cerro Jefe, a few kilometers northeast of Panama City.

PANAMÁ: Finca Indio, along Río Casicadas, Cerro Jefe, high climbing along stream; *D'Arcy 3951*, 5233 (both MO). Cerro Jefe, 700 m, epiphytic shrub, *Dressler 3773* (DUKE, K, MO, MPU, PMA).

2. **Markea neurantha** Hemsl., Biol. Centr. Amer., Bot. 2: 429. 1882. TYPE: Costa Rica, *Endres 534* (K).

Merinthopodium neuranthum (Hemsl.) Donn. Sm., Bot. Gaz. (Crawfordsville) 23: 12, *tab. 1.* 1897.

Shrub, terrestrial or hemi-epiphytic, often high in the trees; twigs (dry) with longitudinally scaling bark and furrows. *Leaves* membranaceous, elliptic, the apex acuminate forming a "drip tip," the base obtuse, acute or acuminate, glabrous except for a few small simple hairs on the midvein beneath, mostly 8–12 cm long and 3–5 cm broad but occasionally much larger, ca. 5 major veins ascending at ca. 45° on each side of the midrib; petioles 1.5–4 cm long, slender, channelled above, ribbed beneath when dry. *Inflorescence* pendant, few- or many-flowered clusters at the end of a long, to 70 cm, slender peduncle which is rough textured with fine simple hairs and fine tuberculae, terminally thickened and stoutish; pedicels 3–10 cm long. *Flowers* with the calyx 2 cm long, lobed almost to the base at anthesis, the lobes ovate-lanceolate, campanulate, glabrous (Panama) or puberulent; corolla campanulate, 3–4 cm long and 2–3 cm across at the mouth, finely puberulent outside, glabrous within, strongly ribbed, the lobes ovate-orbicular; filaments filiform, inserted ca. 5 mm above base of corolla tube, anthers

elongate, 10–13 mm long and 1–3 mm wide, apiculate, the connective dorsally marked when dry, thecae opening fully, exserted; ovary conical, ca. 5 mm tall, immersed in a ring of nectary(?) ca. 1.5 mm tall, stylar base slightly enlarged, style slender, stigma large, exserted. *Berry* ovoid-conical, about as long as the calyx with a conspicuous stylar scar.

This species ranges from Chiriquí through Costa Rica. It is similar to *M. dressleri*, but the flowers are smaller. In Costa Rica there are plants of this or perhaps of a closely related species with tomentose calyces. Flowers are reported as green tinged with purple at the base. Flowers of *M. dressleri* are all green outside but purple inside. Fruiting pedicels of *Kirkbride & Duke* 887 are elongate, 4.5 and 7 cm long.

BOCAS DEL TORO: Without locality *von Wedel 212* (GH, MO). Water Valley, *von Wedel 802* (GH, MO). CHIRIQUÍ: Rain forest, Bajo Chorro, Boquete District, 6,000 ft, *Davidson 184* (A, F, MO). Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, premontane rain forest (oak), *Kirkbride & Duke* 887 (MO). Cerro Horqueta cloud forest, 6,500 ft, *von Hagen & von Hagen 2075* (MO).

B. Section **Megalandra** D'Arcy.[24] TYPE: *Metternickia megalandra* Dun. (= *Markea megalandra* (Dun.) D'Arcy).

3. **Markea crosbiana** D'Arcy.[25] TYPE: Panama, *Dwyer et al. 430* (MO).

Shrub to 3.5 m tall; twigs stout, slightly angled, pilose with stout, white, antrorsely curved hairs, soon glabrescent. Leaves clustered and appearing verticellate, coriaceous, glabrous, elliptical, the apex blunt acuminate with a small "drip tip," the base acute or obtuse, very uniform in size and appearance, 7–9 cm long, 2.5–4 cm across, the margins revolute, lateral veins obscure, 4–5 on each side of the prominent midvein; petioles short, ca. 5 mm long, glabrous, drying with conspicuous corky bars. *Inflorescence* a solitary terminal flower; pedicels stout, ca. 13 mm long, tomentose in the lower portion, warty in the distal portion. *Flowers* with the calyx ca. 5 cm long, glabrous except for a few hairs at the very base, strongly angled, somewhat inflated, splitting ca. ⅓ the way down, the lobes lanceolate, the base of the calyx 2 cm across from angle to angle; corolla glabrous without, tubular-narrowly craterform, ca. 10 cm long, the cup 3 cm across, becoming tubular; anthers slender, ca. 2 mm thick and 12 mm long. *Fruit* unknown.

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[24] Section *Megalandra* D'Arcy, sect. nov. Distinguitur calyce succulenti in statu flori parum fissenti, fructu usque ad imum fissenti; ovario supero; foliis latis, coriaceis, infra subtiliter sive certe glanduloso-punctulatis.

In addition to the two species found in Panama, this section includes the following: *M. uniflora* Lundell, *M. venosa* Standl. & Mort., *Solandra coriacea* O. Kuntze, *S. odorifera* Cuatrec. and perhaps others. It may be generically distinct.

[25] *Markea crosbiana* D'Arcy, sp. nov. Arbor, an epiphiticus, usque ad 3.5 m altus, distingutur. Foliis verticillastris, coriaceis, glabris, subter minute punctulata, venis prominentibus, supra obscuris, marginibus revolutis, infra 7–9 cm longa, 2.5–4 cm lata. Floribus singularis, pedicello crasso, 13 mm longo, tomentoso, supra verrucoso, calyce 5 cm longo, 2 cm lato, glabrato, valde angulato, aliquot inflato, superne ⅓ fissidenti lobos lanceolatos, corolla extus glabra ca. 10 cm longa, limbo 3 cm lato, tubuloso, antheris gracilibus 2 mm crassis 12 mm longisque. Fructus haud suppetunt. Nomen Marshalli R. Crosbyi muscorum plantarumque Panamensium collectoris scrutioris designatur ad hanc *Markeam*.

This species is known from a single herbarium specimen from which the apex of the corolla with its lobes is missing. Although similar to *M. uniflora* Lundell of Mexico and to *M. venosa* Standl. & Mort. of Costa Rica, *Markea crosbiana* differs from both: the first bears its flowers on elongate, 6–8 mm, pedicels, and the second has calyces only ca. 2.5 cm long.

CHIRIQUÍ: Cerro Horqueta NW of Boquete, 5,000–5,800 ft, trail to lower edge of cloud forest, *Dwyer et al. 430* (MO).

4. **Markea megalandra** (Dun.) D'Arcy, Phytologia 25: 116. 1973.

Metternickia megalandra Dun. *in* DC., Prodr. 13(1): 595. 1852. TYPE: Colombia, *Mortiz 827* (BM, G-DC; MO, US, photos).
Markea leucantha Donn. Sm., Bot. Gaz. (Crawfordsville) 21: 116–7. 1901. LECTOTYPE: Costa Rica, *Cooper 5887* (A, K, NY, US).
Metternichia werklei Schum. *ex* Bois, Rev. Hort. 82: 149. 1910. TYPE: Costa Rica, *Werckle s.n.* (?B, not seen; MO, photo).
Merinthopodium leucanthum (Donn. Sm.) Blake, Contr. Gray Herb. 52: 86. 1917.
Markea suaveolens Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 22: 171. 1940. TYPE: *Lawrance 751* (A, F, MO).
Solandra megalandra (Dun.) Killip & Pittier *in* Pittier et al., Cat. Fl. Venez. 2: 353. 1947.

Shrub, hemi-epiphytic forming large clumps in trees; twigs glabrous. *Leaves* coriaceous, glabrous, minutely punctate beneath, mostly 7–10 cm long and 3–5 cm broad, the major veins 5–6 on each side of the midvein, prominently elevated except for the smooth distal portion of the lamina, elliptic, apically rounded or slightly acuminate, basally acute or slightly acuminate, the margins revolute; petioles 1–2 cm long. *Inflorescence* a reduced raceme on a sometimes thickened and elongate peduncle, often appearing clustered at the ends of the branches; pedicels 1 cm long, rusty pubescent with short simple hairs, soon glabrescent. *Flowers* fragrant, the calyx fleshy, campanulate, contracted towards the top, ca. 10 mm long, lobed ⅓ the way down in flower, 4–5 lobed, the lobes unequal, splitting almost to the base in fruit and becoming coriaceous or woody with conspicuous corky warts; the corolla white (purplish) becoming yellow with age, 5 cm long, funnelform-campanulate, 2–3 cm across at the mouth, conspicuously ribbed, the lobes ca. 10 mm long, not strongly recurved, the tube pubescent at the base within; filaments inserted at the base of the corolla tube, pilose at point of insertion, the anthers elliptical, ca. 4 mm long, exserted; the ovary partly inferior, a ring of nectary(?) tissue conspicuous above the top of the receptacle as an annulus on the ovary. *Fruit* (?immature) globose, ca. 14 mm across, drying brown, with a prominent apical stylar scar.

Within *M. megalandra* there is considerable variation in length of calyx: the type collection has a calyx 25 mm long, while the type of *Markea suaveolens* has a calyx only 7 mm long. There appears to be a continuous range within these two extremes, most plants having calyces about 13 mm long.

Markea megalandra occurs from Mexico (Chiapas) to Venezuela. It is a species mainly of middle and upper elevations.

CHIRIQUÍ: Rain forest, Bajo Chorro, Boquete, 6,000 ft, trees, *Davidson 192* (A, MO, US), *263* (A, F, MO, US). Rain forest, Chiquero, Boquete, 5,500 ft, *Davidson 529* (US).

C. Section **Granatense** D'Arcy.[26] TYPE: *M. ulei* (Damm.) Cuatrec.

Ectozoma Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 191. 1849.

5. **Markea ulei** (Damm.) Cuatr. Fedde Repert. 61: 78. 1958.

Ectozoma ulei Damm., Bot. Jahrb. (Syst.) 37: 170. 1905. SYNTYPE: Peru, *Ule 5729a* (G; MO, photo).
Markea panamensis Standl., Jour. Arnold Arbor. 11: 127. 1930. TYPE: Panama, *Bangham 543* (A, F, G, MO, US).
M. dimorpha Mort., Proc. Biol. Soc. Washington 58: 1. 1945. TYPE: Colombia, *Metcalf & Cuatrecasas 30198* (A, F, MO, US).

Shrub, hemi-epiphytic; branches slender and elongate, often bearing slender adventitious roots, the bark green drying scaly brown. *Leaves* mostly clustered near the ends of the branches or on short spurs, to 15 cm long, elliptic or ovate, sometimes oblique, mostly broadest above the middle, apically acuminate, basally narrowed, rounded or acuminate, glabrous; petioles ca. 10 mm long. *Inflorescence* a reduced panicle or raceme, several-flowered on stout, sparingly branched axes 1–3 cm long; pedicels 6–15 mm long. *Flowers* small, the calyx 5–7 mm long, 5-angled in bud, lobed almost to the base, vestite with minute, dense, straight hairs; corolla milky to whitish, often with areas colored by minute purplish hairs, 10 mm long, campanulate, 5-angled, exceeding the calyx by more than half its length, the 5 lobes recurved; anthers sub-sessile, elongate-ovoid, included, opening longitudinally from the apex, 4–5 mm long. *Fruit* yellow, ca. 10 mm long, ovoid-conical, barely exserted from the slightly accrescent calyx lobes.

This species is distinct in its small flower, deeply lobed calyx, and ovoid, apiculate anthers. It may not be congeneric with *Markea coccinea* Rich.

Markea ulei ranges from central Panama into Peru. It occurs in dense shade at various levels in mature forests and also in the forest canopy and openings in full sun.

Markea pavonii (Miers) D'Arcy is superficially similar to *Markea ulei*, but the calyx is lobed only a short way, resembling that of *M. megalandra*. The leaves are coriaceous but not punctate beneath as those of sect. *Megalandra*. It is known only from the type collection (Ecuador, *Pavon s.n.* (BM)).

CANAL ZONE: Mojinga swamp near mouth of Río Chagres, below 1 m, *Allen 862* (MO). Barro Colorado Island, *Aviles 53* (F, MO); *Bangham 543* (A, F, G, MO, US); *Carpenter 55* (F); *Croat 6031, 8041, 8239, 8498, 8911, 11477* (all MO); *D'Arcy 3926, 3946* (both MO); *Ebinger 563* (MO, US); *Foster 1057* (DUKE, PMA); *Kenoyer 619* (F); *Shattuck 272* (F, MO); *Wilson 60* (F, MO); *Woodworth & Vestal 599* (A, MO). COLÓN: Near Guasimo, forested area along Río Miguel de la Borda, *Croat 9912* (MO). Santa Rita lumber road ca. 15 km E of Colón, *Dressler & Lewis 3700* (MO). East Ridge (Santa Rita), *Duke 15295* (MO). Santa Rita Ridge, 4–5.5 mi. E of Transisthmian Highway, advanced secondary forest, *Lewis et al. 5290* (ADW, BIRM, C, MO). Santa Rita Ridge, end of road from Transisthmian Highway ca. 10 mi. from highway, advanced secondary forest, *Porter et al. 4820* (MO). DARIÉN: Between Quebrada Venado and Peje Swamp on headwaters of Río Tuqueza, *Bristan 1010* (BIRM, MO). Forest near Pidiaque peak, 800–1,000 ft, *Duke 8069* (MO). Cuipo

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[26] Section *Granatense* D'Arcy, sect. nov. Distinguitur floribis parvis, calyce profunde lobato, antheris ovoideis, apiculatis.

forests near Santa Fé, *Duke 12268* (MO). Río Balsa between Manene and Tusijuanda, *Duke 13542* (MO). Tumaganti, 300 m, *Duke 14161* (MO). Without locality, *Duke & Bristan 8197* (OS). Manene to mouth of Río Cuasi, *Kirkbride & Bristan 1454* (MO). Along Río Sambú, above tide limit, *Pittier 5566* (F). Periaque camp at river, *Tyson et al. 4748* (MO). PANAMÁ: 19 mi. N of El Llano on road to Carti (San Blas), 500 m, *Busey 907* (C, MO, P, PMA, W, WIS). Forests along headwaters of Río Corso, 500 ft, *Duke 11914, 11945* (both MO). N of El Llano, 500–800 m, *Gentry 5580* (MO). SAN BLAS: Near stream above Puerto Obaldia, *Gentry 1542* (MO, NY).

14. NICOTIANA

Nicotiana L., Sp. Pl. 180–1. 1753; Gen. Pl., ed. 5. 84. 1754. TYPE: *N. tabacum* L.[27]

Erect *herbs* or *shrubs* to 3 m tall, often glandular or viscid pubescent, unarmed. *Leaves* entire, sessile or petiolate, sometimes large; minor leaves often present as auricles or cauline stipule-like processes. *Inflorescence* a terminal, many flowered panicle, bracteate, and the pedicels bracteolate, articulating at the base. *Flowers* regular or somewhat zygomorphic, 5-merous; calyx campanulate, somewhat accrescent but not enclosing the fruit; mostly 5-lobed, the lobes short or elongate, persistent; corolla tubular, salverform or elongate, campanulate, variously colored, prefloration contorted-plicate, rarely imbricate; stamens 5, equal or not, filaments equally or unequally inserted at various levels in the corolla tube, often pubescent, sometimes geniculate, anthers included or nearly so, dehiscent longitudinally, 2-thecate, the connective apparent or not; ovary 2-loculed on an annular hypogenous, sometimes nectiferous disc, the placentae axillary, somewhat proliferated, ovules numerous, anatropous, stigma included or exserted. *Fruit* a chartaceous or coriaceous capsule, dehiscent apically by septicidal and locucidal slits; seeds many, minute, globose or often prismatic, the embryo small, straight, curved, bent or arched. Chromosomes mostly $n = 12$ or 24.

A genus of about 60 species, centered in higher elevations of South America but with groups of species in Mexico, Australia and the South Pacific as well as lowland South America. The genus is not native to Central America with the exception of one species in Guatemala and southern Mexico. The species treated here is widely cultivated and naturalized in many parts of the world.

Nicotiana is one of the world's most important drug plants with a long tradition in the regions where it is native as well as in parts of North America where it was dispersed by pre-Columbian man. It was introduced to Europe and Africa and other parts of the New World very soon after Spanish and Portuguese contact and today is a major crop plant in a number of countries. There is today a much larger acreage devoted to cultivation of tobacco than to any other drug plant. Taxation, moral arguments, and health considerations tend to diminish total production and usage, but the strong attraction of the odor of smouldering tobacco and the addictive consequences of its use foretell the continued use of

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[27] For a list of synonyms see Goodspeed (1954); none of these synonyms has been used for Panamanian plants.

this plant as a social drug. Several species of *Nicotiana* are employed as tobacco, the one grown in Panama being the most widespread in world use and commerce.

Nicotiana is closely related to *Petunia* among the Salpiglossidae. Goodspeed believed it to be intermediate between or at least closely related to *Cestrum* and *Petunia*. The structure of the inflorescence with its bracts, bracteoles and its generally clasping leaf bases are good distinguishing characters.

The name is taken from the name of Jean Nocot de Vellemain, French Minister to Lisbon, 1560, and was long the traditional French name for the plant.

Useful reference:

Goodspeed, T. H. The genus *Nicotiana*. Chron. Bot. 16. 1954.

1. **Nicotiana tabacum** L., Sp. Pl. 180. 1753. TYPE: Herb. Linn. 245.1 (LINN).[28]

Stout, erect, viscid ephemeral or short-lived *perennial* to 3 m tall; stems stout, sparingly branched, very leafy. *Leaves* large, to 50 cm long, elliptic or obovate, apically acute or acuminate, basally narrowed into a winged petiole and expanded to give the appearance of 2 foliaceous stipules, the petiole and its foliose wings decurrent on the stem. *Inflorescence* a large, many-flowered, open, terminal panicle to 30 cm long with clasping bracts and linear to foliaceous bracteoles; pedicels slender, erect or nodding, to 2 cm long, mostly erect in fruit. *Flowers* with the calyx campanulate-tubular, 10–18 mm long, irregularly lobed ca. ¼ the way down, the lobes acute, the tube slightly accrescent; corolla variously pastel colored, obconic with an expansion about ⅔ the way up, ca. 1 cm broad at the mouth, the lobes pointed, the top 2–3 cm across; 4 stamens subequal, one somewhat shorter, the filaments inserted equally at the base of the corolla throat, pubescent except near the apex; stigma globose-capitate, somewhat exserted. *Capsule* exserted about ½ the way from the calyx (or included, Goodspeed), 15–20 mm long, ovoid, the main openings septicidal; seeds globose or ellipsoid; ca. 0.5 mm long, ridged, brown; embryo straight.

This species is cultivated in various parts of Panama. The markets in Panama City display considerable leaf from Chiriquí. Near Chepo is a substantial acreage of tobacco grown under modern techniques of planting, cleaning, and fertilizing. *Nicotiana tabacum* is only sparingly spontaneous in Panamá.

CHIRIQUÍ: Chiriquí Viejo Valley, *White 103* (MO). PANAMÁ: Large plantation ca. 4 mi. SW of Chepo, *D'Arcy 3945* (MO). Cultivated on road from Chepo to El Llano, *Tyson 4121* (SCZ).

15. PETUNIA

Petunia Juss., Ann. Mus. Paris 2: 215, *tab. 47*. 1803. TYPE: *P. parviflora* Juss.[29]

Viscid, unarmed *herbs* or *shrubs*. *Leaves* simple, entire, sessile or rarely petiolate; minor leaves absent. *Inflorescence* a short raceme with paired, equal bracts, the flowers remote and appearing solitary with paired, equal bracteoles,

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[28] For names to be placed in synonymy see Goodspeed (1954: 372). None of these names has been employed in Panama.

[29] For a list of generic synonyms see Fries (1911). Synonyms have not been used for Panamanian material.

the pedicels sturdy, articulating at the base. *Flowers* minute to large and showy, 5-merous, slightly irregular, calyx campanulate or tubular-salverform, strongly nerved, lobed more than halfway to the base, the lobes sometimes subfoliaceous; corolla salverform, tubiform or funnelform, prefloration induplicate, the limb sinuate-lobed; stamens equal or not, the filaments inserted below the middle of the corolla tube, sometimes geniculate, the anthers included, ovoid, versatile, 4-thecate, dehiscing longitudinally; ovary 2-loculed, the ovules many on axile placentae. *Fruit* a dry capsule dehiscing septicidally in the apical portion, many-seeded; seeds minute, globose, reniform or prismatic, foveate; embryo straight or slightly curved.

A genus of about 35 species scattered in ultramontane South America and centered in southeastern Brazil, one species disjunct in northern Mexico and the southern United States. This genus, together with the similar genus *Nicotiana*, represents an element possibly primitive to the tribe Salpiglossidae. A discussion of evolutionary relationships appears in Goodspeed, The Genus *Nicotiana* (Chron. Bot. 16. 1954). *Petunia* is distinguished from *Nicotiana* in the bracts and bracteoles being always paired, leading to a frequent statement that *Petunia* has opposite leaves. In addition, the corolla mouth in *Petunia* is not usually so contracted as in *Nicotiana*. *Petunia violacea* is widely cultivated for ornament and many large-flowered and showy cultivars, some involving polyploidy, are available from northern seed houses.

The name is derived from "petum," an aboriginal name for tobacco.

Useful reference:

Fries, R. E. Die Arten der Gattung *Petunia*. Kongl. Svensk. Vetenskapsakad. Handl. 46. 1911.

1. **Petunia violacea** Lindl., Bot. Reg. *tab. 1626*. 1833. TYPE: (not seen).[30]

Herb or low *shrub* to 60 cm tall, branching near the base and erect or sprawling, aromatic and densely viscid-pubescent; stems often winged. *Leaves* ovate, lanceolate or spatulate, 2–5 cm long, acute apically, narrowed basally, pilose overall; petioles short or wanting. *Inflorescences* with the peduncles to 30 cm long, bracts and bracteoles foliaceous, 0.5–2 cm long, the pedicels 1–4 cm long, pilose, elongating in fruit. *Flowers* showy, the calyx unequally-lobed to near the base, the lobes sometimes large and foliaceous, 8–15 mm long, erect or spreading and becoming broader in fruit; corolla large but variable in size, 2–5 cm long, salverform, the tube narrow, strongly nerved, hirsute outside, glabrous within, the limb with 5 rotund lobes, pubescent on the nerves outside; stamens subequal, 2 slightly longer and one shorter, the filaments geniculate, glabrous, inserted ca. ⅔ down the tube, straight above, the anthers alike, ellipsoid, ca. 3 mm long; ovary elongate-conical, glabrous, the style geniculate on top, glabrous, the stigma a partly exserted, 2-lobed disc. *Fruit* 10 mm long, stramineous, the foveate placenta persistent after the seeds have fallen; seeds minute, globose-prismatic, foveate, dark brown.

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[30] For a list of synonyms see Fries (1911). Synonyms have not been used for Panamanian material.

Petunia violacea, a native of Brazil, is widely cultivated in temperate countries and upland parts of the tropics. Only one collection is known from Panama. It is probably a garden escape. Residents of the Chiriquí mountains say they cultivate this species from time to time from imported seed.

The one Panamanian collection bears considerable resemblance to *Petunia occidentalis* Fries, a species Fries considered localized in Bolivia and Argentina. Examination of a photo of the type (Fries, 1911) and material identified by Fries suggests that *P. occidentalis* is not distinct from *P. violacea*. For a discussion of the ancestry of the garden Petunia, see Ferguson and Ottely (Amer. Jour. Bot. 19: 385. 1932).

PANAMÁ: Sabanas, *Bro. Paul 50* (US).

16. PHYSALIS

Physalis [Diosk.] L., Sp. Pl. 182–184. 1753; Gen. Pl., ed. 5. 85. 1754. TYPE: *P. alkekengi* L.

[*Physallis* Diosk., Mat. Med., Paris. 1516, not seen.]
Alkekengi Mill, Gard. Dict., abr. ed. 1754. TYPE: Not designated.
Herschellia Bowd., Excurs. Madeira 159. 1825. TYPE: *H. edulis* Bowd. (Referred to synonymy here by Index Kewensis.)
Eplateia Raf., Sylv. Tell. 57. 1838. TYPE: *Physalis arborescens* L.
Epetorhiza (Don) Steud., Nom., ed. 2. 1: 556. 1840. TYPE: Based on *Physalis* sect. *Epeteiorhiza* G. Don, Gen. Syst. 4: 449. 1837–8. TYPE: Not designated.

Unarmed *herbs* or rarely *shrubs*, pubescent with simple, often glandular or viscid, rarely dendritic hairs, sometimes sarmentose. *Leaves* simple and entire, shallowly toothed or lobed; petiolate; minor leaves when present resembling the major leaves. *Inflorescence* axillary, bracts obsolete, pedicels solitary or rarely in small fascicles, often elongating and cernuus in fruit. *Flowers* perfect and mostly nodding, calyx valvate, 5-lobed, accrescent and loosely enveloping the fruit or nearly so, remaining flexible or becoming woody-chartaceous; corollas yellow (Panama), often marked in the throat, funnelform or rotate, sometimes reflexed, induplicate-valvate, the margin nearly entire or with 5 short, ovate-deltoid to subulate lobes; stamens mostly equal, the filaments inserted in the corolla tube, pubescent or not, the anthers all fertile, yellow or with various amounts of blue or purple and drying greenish, oblong-ovoid, basifixed, opening by longitudinal slits, in some species twisting and curling, the connective not apparent; ovary 2-locular, the many ovules anatropous, the style exserted, the stigma small. *Fruit* a juicy or fleshy, slightly stalked, many-seeded berry, glabrous but sometimes viscid; seeds compressed, slightly rugose, the embryo circinnate at the periphery of the seed.

Physalis has its greatest number of species in Mexico, but some species are found in Central and South America and a few occur in the Old World. About 90 species are known. Most of the species now found in the Old World and probably those in Panama are widespread weeds. These plants are most common in ruderal sites. The berries are used for food, some species being cooked and others eaten out of hand. *Physalis peruviana* is a crop plant in South Africa,

and *P. alkekengi*, a European species, is cultivated for ornament in temperate countries. Duke reported in the *Darien Ethnobotanical Dictionary* that "the fruits are eaten raw or cooked, especially as an additive to stews. They are sometimes made into preserves by cooking in palm syrup."

The name of the genus comes from a Greek word meaning bladder or bubble. These plants now go under a number of common names, *e.g.*, "ground cherry" (English), "sacabuche" (Puerto Rico), "tope-tope" (Dominican Republic), "suevos," "huevo de tortuga," "huevito," "bomba" (Salvador), "miltomate" (Guatemala), "uchuba" (Antioquia), "hierba de sapo," "topetón" (Panama).

Useful references:

Waterfall, U. T. A taxonomic study of the genus *Physalis* in North America north of Mexico. Rhodora 60: 107–114; 128–142; 152–173. 1958.

———. *Physalis* in Mexico, Central America and the West Indies. Rhodora 69: 82–120; 202–239; 319–329. 1967.

a. Stems glabrous except for emergent parts and occasionally near the nodes.
  b. Stout white hairs emerging from teeth or enations on the calyx ribs ..... 6. *P. lagascae*
  bb. Plants without stout, white long hairs on the calyx.
    c. Most leaves less than 2 cm long; leaves, stems, fruiting calyces, etc., evenly clothed with stiff, microscopic hairs; fruiting calyces to 20 mm long, 5-angled ..... 7. *P. minuta*
    cc. Leaves mostly more than 3 cm (to 15 cm) long; pubescence of minute, sparse, spreading hairs; fruiting calyces mostly longer than 20 mm, 5-angled or not.
      d. Calyx lobes linear-lanceolate just after flowering, twice or more the length of the tube ..... 2. *P. cordata*
      dd. Calyx lobes deltoid lanceolate, never much exceeding the tube ..... 1. *P. angulata*

aa. Stems pubescent along much of the length (if glabrous in extreme age, then calyx 5-angled).
  e. Stems mostly shaggy pubescent, at least some hairs of stems or petioles 1 mm long.
    f. Fruiting calyx strongly angled; stems mostly densely hairy.
      g. Corollas with strongly contrasting dark markings in the throat ..... 9a. *P. pubescens* var. *pubescens*
      gg. Corolla with faint or no dark markings in the throat ..... 9b. *P. pubescens* var. *hygrophila*
    ff. Fruiting calyx not strongly angled; stems sparingly hairy.
      h. Calyx pilose; anthers yellowish; fruit not sticky ..... 3. *P. gracilis*
      hh. Calyx lightly pubescent; anthers bluish; fruit sticky ..... 8. *P. philadelphica*
  ee. Stems puberulent, no 1 mm long hairs present.
    i. Flowering calyx 2 mm across or less at the base of the lobes; most leaves 2 cm long or less ..... 7. *P. minuta*
    ii. Flowering calyx more than 2 mm across at the base of the lobes; most leaves 2 cm or more long.
      j. Fruiting calyx glabrous during and just after anthesis; calyx lobes narrowly lanceolate ..... 2. *P. cordata*
      jj. Fruiting calyx pubescent; calyx lobes deltoid to lanceolate.
        k. Pubescence of leaves mainly confined to margins and veins; leaves drying translucent, fruiting calyces rarely to 30 mm long ..... 4. *P. hirsuta*
        kk. Plants evenly puberulent overall with short, greyish hairs; leaves opaque; fruiting calyces sometimes large (40 mm long).
          l. Calyx with strongly contrasting dark markings in the throat; anthers purple or blue ..... 9a. *P. pubescens* var. *pubescens*
          ll. Calyx with faint or no dark markings in the throat; anthers mostly yellow ..... 5. *P. ignota*

1. **Physalis angulata** L., Sp. Pl. 1: 183. 1753. TYPE: Herb. Linn. 247.9 (LINN).

Sprawling or erect *herb* to 1 m tall, stems angled, glabrous except for minute appressed hairs on the youngest parts. *Leaves* to 10 cm long, ovate or elliptic, apically acute or acuminate, basally acuminate and often oblique, the margins entire, sinuate, dentate or irregularly incised, glabrate; petioles ⅓–½ as long as the leaves. *Pedicels* 5–12 mm long, mostly longer than the calyces, puberulent with fine antrorse hairs. *Flowers* with the calyx 3–5 mm long, 2–4 mm across at the base of the lobes, glabrous except at the margins and tips of the lobes, the lobes broadly acute; corolla usually without a contrasting eye, 4–10 mm long, sometimes reflexing backwards when fully open; stamens sometimes unequal, the filaments slender, the anthers bluish, sometimes fading yellow or drying or curling at maturity, 2–2.5 mm long. *Fruits* on slender pedicels mostly 10–25 mm long; fruiting calyx 10-angled or terete, 20–30 mm long, glabrous, often drying reticulate-veined or with a purplish cast; berry globose, 10–12 mm across.

The fruiting calyces of *P. angulata* have inconspicuous angles, and the name is derived from angles on the branches which are indeed conspicuous. Mature fruits on material from Panama and most material from North America have completely glabrous calyces. Occasionally plants are encountered with a few small hairs on the calyx ribs and minute puberulence on the main veins of mature leaves. The type specimen, cited above, is one of these plants, essentially glabrous but not entirely so.

Features for recognition of *P. angulata* are the overall lack of pubescence, the terete or 10-angled calyces, and the corolla usually without a constrasting eye. This species lacks the stout white hairs on parts of the calyx that separate *P. gracilis* or *P. lagascae*, and the calyx lobes are never much more than equal the length of the tube in contrast to *P. cordata*.

This is the commonest and most widespread species of *Physalis*. It has wide ecological tolerance but is perhaps best suited to ruderal habitats and other sites of disturbance. It ranges from Manitoba to southern Argentina and is widespread in the Old World.

BOCAS DEL TORO: Region of Almirante, *Cooper 127* (F). Changuinola Valley, *Dunlap 84a* (F). 5 mi. N of Changuinola on the Changuinola River bank, next to the banana dump, *Lazor et al. 2455* (F, FSU, GH, K, MO, NY, SCZ, UC, US). Town of Changuinola, field with foundation pits dug and lightly tilled followed by spot grazing, *Lazor et al. 2598* (FSU). CANAL ZONE: 2 mi. S of Fort Sherman, *Blum & Tyson 2010* (FSU, MO). Along road between Gatun & Fort Sherman on dry open recently graded ditch, *Croat 15389, 15390* (both MO). Madden Dam area, Boy Scout Road, *Dwyer & Lallathin 8817* (MO). Barro Colorado Island, *Ebinger 594* (US). Chagres, *Fendler 247* (MO, US). Near Culebra, 50–290 m, *Pittier 2227* (F, US), *4782* (F, GH, US). CHIRIQUÍ: Quebrada del Medio, 2 km N of Punta de Burica, *Busey 759* (C, MO). COCLÉ: El Valle de Antón, *Aquilar 58* (MO). COLÓN: ¼ mi. N of María Chiquita on road to Portobelo, *Croat 11343* (MO). DARIÉN: Along airstrip at El Real, *Lazor & Correa 3409* (FSU, MO, SCZ). Near El Real, *Stern et al. 453* (GH, MO, US). HERRERA: Between El Potrero and Las Minas, open weedy roadside, *D'Arcy & Croat 4139* (MO). LOS SANTOS: Las Tablas, beach, *Dwyer 1023* (MO). PANAMÁ: Main camp, weed in lawn, San José Island, *Johnston 993* (GH). Dry woods, Taboga Island, *Killip 3143* (MO). With *Ricinus communis* and cultivated bananas on brushy, weedy sandbar along Río Pacora, 1 km upstream from Pacora, *Nee & Mori 3620* (MO). Between Río Pacora and Chepo, roadside savanna, *Porter et al. 5126B* (F, MO). Macapale Island in Madden Lake, common near

top of flood plain, *Tyson 5500, 5506* (FSU, MO). Marsh area 2 mi. S of Tocumen Airport, infrequent in marshy grazed area in sun, *Tyson & Clewell* 5925 (DUKE, FSU, MO).

2. **Physalis cordata** Mill., Gard. Dict., ed. 8. 1768. TYPE: Vera Cruz, *Houston s.n.* (BM).

Erect or sprawling short-lived *herb* to 80 cm tall; stems glabrate with some minute, antrorsely curved hairs often present. *Leaves* to 8 cm long, broadly ovate or elliptic, apically acuminate, basally rounded or truncate, the margins shallowly toothed, glabrate with some puberulence along the veins; petioles slender, 3–9 cm long, mostly shorter than the leaves; minor leaves present. *Pedicels* slender, minutely puberulent, about as long as the flowering calyx. *Flowers* with the calyx 3–6 mm long, 2–3 mm in diameter at the base of the lobes, the mouth of the tube sometimes contracted, glabrous except on the angles, the lobes narrowly deltoid, slightly longer than the tube, soon after flowering becoming 2–3 times as long as the tube; corolla with a contrasting pubescent eye, 5–10 mm long; filaments pubescent, the anthers bluish, 1.8–3 mm long. *Fruits* on slender pedicels not exceeding the calyx; fruiting calyx 5-angled, 25–30 (–45) mm long, glabrous, the lobes not exceeding 10 mm long; berry globose, 7–15 mm across.

This species is easily mistaken for *P. angulata* from which it differs in the proportions of the calyx teeth and lobes, best seen when the young fruiting calyx is less than 11 mm long. It differs also in the 5-angled calyx, but this character is not always evident in dried material.

Physalis cordata usually is found in moist, partially shaded sites in regions occasionally subjected to drought. It ranges from Panama to central Mexico and is found in both the Greater and Lesser Antilles. It may occur in South America. While most collections are from the lowlands, *P. cordata* has sometimes been collected from middle and upper elevations.

BOCAS DEL TORO: Chiriquí Lagoon, *von Wedel 1167* (GH). CHIRIQUÍ: South side of Cerro Pando, 6,000 ft, along path in abandoned cultivation, *D'Arcy 5392* (MO). Weedy pasture, La Popa above Boquete, 5,200 ft, *D'Arcy & D'Arcy 6413* (C, COI, MO, PMA, UCWI). COCLÉ: Las Delicias, *Carleton 223* (NY, US). COLÓN: Wooded hillside between France Field, C.Z. and Cativa1, *Standley 30236* (US). DARIÉN: Edge of pasture and stream near junction Río Perre Cenico and Río Pirre, *D'Arcy 5521* (COI, MO, MPU). 2–3 mi. SE of El Real, *Duke 4860* (F, MO). Periaque camp at river, *Tyson et al. 4738* (FSU, GH, MO, SCZ). 1 mi. N of Río Sabana, *Tyson et al. 4803* (MO; the specimen at SCZ with this number is *P. pubescens* var. *hygrophila* (Mart.) Dun.). LOS SANTOS: Río Tonosí, vicinity of Tonosí, gravel river bed and forest edge, *Lewis et al. 1579* (COI, F, MO, MPU). PANAMÁ: Edge of forest, top of ridge N of El Llano, *D'Arcy & D'Arcy 6039* (C, MO, P, PMA, UCWI). Piria, *Duke 14424* (OS, US). Weed patch beside road near Cerro Azul, 2,000 ft, *D'Arcy & D'Arcy 6213* (ADW, BIRM, C, CAL, COI, COL, CORD, DAO, DUKE, F, FSU, G, GH, K, L, LE, M, MO, MPU, NY, P, PMA, POM, PRE, R, TH, UCWI, US, VEN, WIS). Common, Tocumen, *Dwyer 4252* (FSU). In total shade, Chepo near river, *Tyson 1415* (SCZ). Río Tatare, *Woodson & Schery 1015* (MO, US).

3. **Physalis gracilis** Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 37. 1849. TYPE: Mexico, *Coulter 1222* (GH).

Erect or scandent *herb* to 1.2 m tall, stems glabrate to villous with conspicuous 1–1.5 mm long hairs, glabrescent below, the pubescence associated with areas

of stem near the slightly swollen nodes, occasionally rooting at the nodes (*Lewis et al. 812A*, MO). *Leaves* to 10 cm long, ovate, apically acuminate, basally rounded or obtuse, the margins subentire, the lamina with scattered short hairs; petioles as long as the leaves or shorter, pubescent on the upper surface. *Pedicels* slender, 7–21 mm long, longer than the flowering calyces and with long, erect and spreading hairs. *Flowers* with the calyx 5–10 mm long, the lobes acute-deltoid, their tips often recurved and upfolded from the midribs, glabrate to conspicuously pubescent with long, erect or spreading hairs; corolla with a contrasting pubescent eye, 9–13 mm long and reflexing open to 16 mm across; filaments slender but somewhat flattened, the anthers yellow or blue, 3–4 mm long. *Fruits* on slender to somewhat thickened pedicels 10–20 mm long, fruiting calyx 10-angled to terete, 20–30 mm long with scattered long hairs which are not particular to the ribs; berry 8–15 mm across.

This species is identified by the long, white, jointed hairs occurring near and at the nodes and on the calyx. Unlike those of *P. lagascae*, the hairs are not associated with the calyx ribs, and those that do occur on the ribs have no suggestion of teeth or calyx enation at their bases. The anthers are larger than those of most Panamanian species, and like *P. angulata*, the calyx is not 5-angled.

Physalis gracilis is found in moist habitats from Bocas del Toro west through Central America to northern Mexico.

BOCAS DEL TORO: Changuinola to 5 mi. S at junction of Río Changuinola and Río Teribe, 100–200 ft, edge of river and railway and adjacent rain forest, *Lewis et al. 812A* (GH, K, MO, NY, UC, US). Chiriquicito to 5 mi. S along Río Guarumo, rain forest by river, *Lewis et al. 1954* (MO).

4. **Physalis hirsuta** Dun. *in* DC., Prodr. 13(1): 445–6. 1852.

P. hirsuta var. *integrifolia* Dun. *in* DC., Prodr. 13(1): 445–6. 1852, = var. *hirsuta*. TYPE: Ohio, *Frank 30* (G-DC).

?*P. hirsuta* var. *repando-dentata* Dun. *in* DC., Prodr. 13(1): 445–6. 1852. LECTOTYPE: Not designated.

P. leptophylla Rob. & Greenm., Proc. Amer. Acad. Arts 29: 389–390. 1894. LECTOTYPE: Mexico, *Wright 1252* (GH); paratypes, Mexico, *Palmer 709* (GH, NY), *Pringle 5455* (GH).

Herb 30–90 cm tall, the stems fine-puberulent with short, 2–3-celled, simple hairs and with scattered, soft, white hairs, 1–2 mm long, or glabrate with one or both of these types of hairs almost wanting. *Leaves* to 8 cm long, ovate, apically acute or acuminate, basally rounded or subcordate, margins entire or irregularly toothed, membranaceous, translucent and green when dry, glabrate except for short hairs on the major veins and leaf margins; petioles often equalling the leaves. *Pedicels* 2–3 mm long, slightly shorter than the calyx. *Flowers* with the calyx 2–4 mm long, loosely pubescent, the lobes acuminate; corolla with a contrasting eye, ca. 8 mm long, glabrate within; filaments glabrous, dorsally flattened, the anthers blue, 1.5–2 mm long. *Fruit* on slender pedicels 5–8 mm long; fruiting calyx ciliate on the ribs, strongly 5-angled, 15–25 mm long; berry 4–8 mm long.

Because of scant material available, the above description is at some points amplified with details from Waterfall's (1967) treatment. Most of the description is taken from *Duke 8734*.

This taxon may be an extreme form of *P. pubescens* with translucent leaves and reduced pubescence. It is so different in general appearance that for the present it is best recognized as a species in its own right. Plants similar to this have been collected from a number of locations in Mexico and the United States as well as at least one station in Guatemala.

The var. *integrifolia* is here designated as the typical variety of the species, and following Art. 26 of the *Code*, its name becomes var. *hirsuta*.

The name *P. hirsuta* is used with hesitation as the earlier name *P. obscura* Michx. (Fl. Bor.-Amer. 1: 149. 1803) may apply. Waterfall (1958) saw the type collection of *P. obscura* in the herb. Michaux (P), but he apparently did not see type material of *P. hirsuta* in the De Candolle herbarium (G-DC), or anywhere else. If he was correct in placing *P. hirsuta* var. *repando-dentata* Dun. into synonymy under *P. obscura* var. *glabra* Michx. (= var. *obscura*), then *P. obscura* may apply. At Geneva (G-DC), there is one specimen (*Frank 30*) supporting var. *integrifolia*, and two labelled as var. *repando-dentata*. The first of these latter is labelled "A Domingue," and while Dunal cited such a specimen in his protologue, he was clearly writing about a plant from eastern North America, so choice of a plant from the Antilles as lectotype is not appropriate. The second specimen, which matches the concept of *P. hirsuta*, employed here, is without designation of source or collector, and without further documentation is not appropriate for a lectotype. A search of other herbaria (*e.g.* MPU) may uncover a suitable lectotype.

In his 1958 treatment of North American species of *Physalis*, Waterfall used the name *P. pubescens* var. *integrifolia* for this taxon, but in 1967 in his Central American treatment, he used the name *P. leptophylla*. An understanding of the biological affinities and range of variation of this taxon will be necessary before a sound choice can be made as to its name.

DARIÉN: Peak ca. 3,000 ft. high between Río Balsa and Río Areti at their confluence, *Duke 8734* (MO, OS).

5. **Physalis ignota** Britt., Mem. Torrey Bot. Club 16: 100–101. 1920. TYPE: Cuba, *Britton & Wilson 5767* (NY, US).—FIG. 15.

P. pentagona Blake, Contr. U. S. Natl. Herb. 21: 20–21. 1922. TYPE: Guatemala, *Blake 7313* (GH, US).

Erect *herb* to 1 m tall, stems stout, evenly covered with short, curved, simple, several-celled greyish hairs. *Leaves* to 12 cm long, broadly ovate or elliptic, apically acute or acuminate, basally rounded or narrowed, mostly oblique, the margin entire or sinuate, rarely toothed, evenly puberulent on the lamina, the major veins puberulent to villous; petioles ½ to as long as the leaves, slender, villous above. *Pedicels* densely vestite, 3–7 mm long. *Flowers* with the calyx 5–8 mm long, 3–6 mm wide at base of the lobes, villous, sometimes viscid, the lobes ovate-lanceolate to narrowly lanceolate and attenuate; corolla unmarked, 6–10 mm long; anthers yellow or blue, 2–2.5 mm long. *Fruits* congested on stout pedicels 7–15 mm long, finely vestite with short erect hairs; fruiting calyx 2.5–5 cm long, coriaceous, strongly 5-angled, evenly puberulent with minute hairs; berry 10–16 mm long.

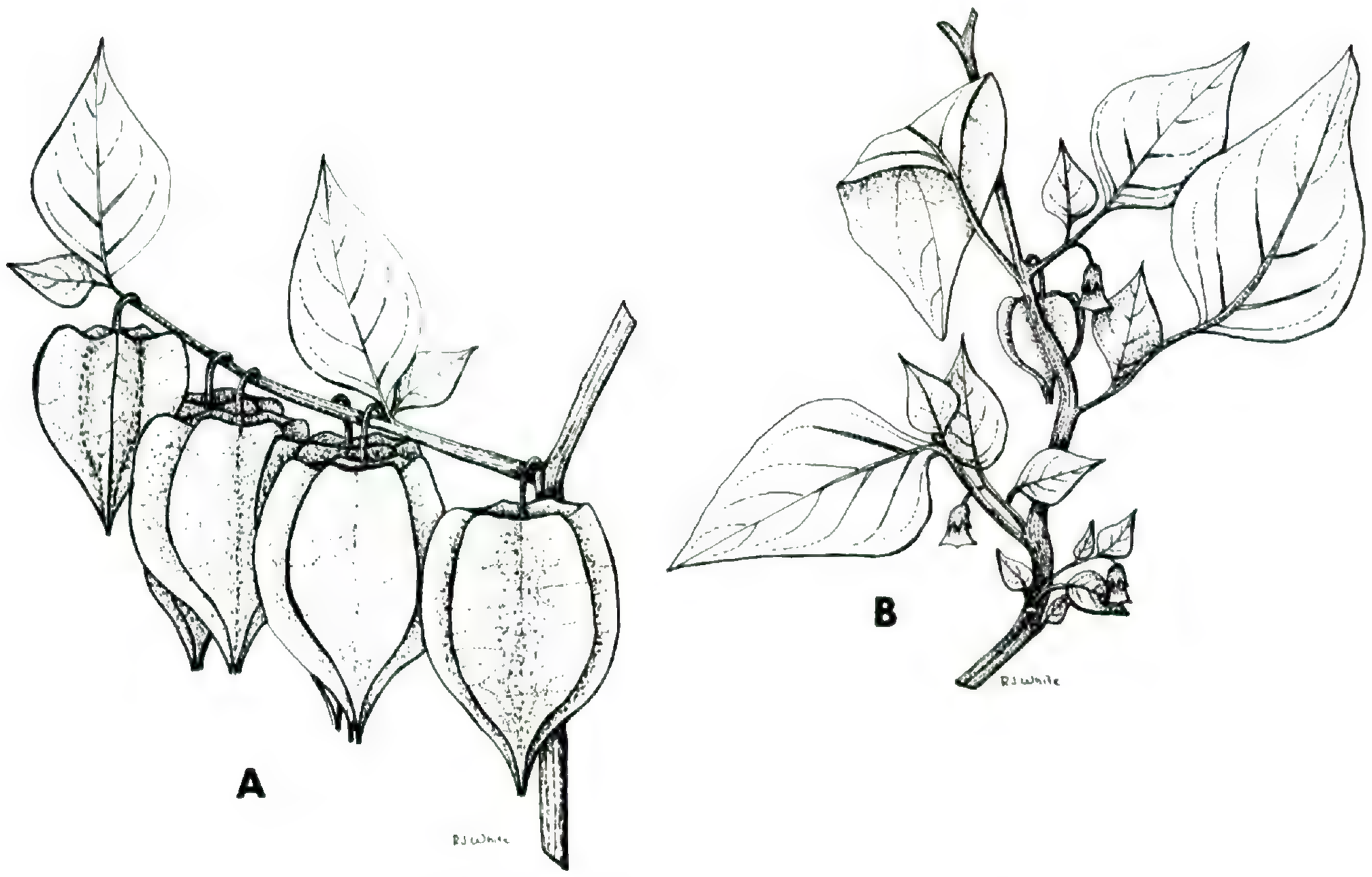

FIGURE 15. *Physalis ignota* Britt.—A. Fruiting branch (× ½). [After *Allen 1136* (MO).]—B. Branch with flowers and fruit (× ½). [After *Porter et al. 5126A* (MO).]

The fruiting calyx of this species may become larger and heavier in construction than in any other species in Panama. The greyish indumentum, sinuate leaf margins and unspotted corollas are good recognition characters for those specimens having smaller fruits. Plants may reach the largest size of any Panamanian *Physalis* species, but they are also capable of blooming and fruiting when only 50 cm tall.

Physalis ignota occurs mainly in sandy or gravelly sites along streams and beaches or in weedy fields. It occurs in the lowlands and ascends to middle and perhaps upper elevations. From Panama it ranges west to Guatemala and north to Cuba.

COCLÉ: 10 mi. E of Natá at Río Grande, frequent in sun, *Tyson 5260* (FSU, MO, SCZ). LOS SANTOS: Monagre Beach 5 mi. SE of Chitré, *Tyson et al. 3003* (FSU, PMA). Los Asientos, arbusto, *Wendehake 42* (DUKE, FSU, MO, PMA). PANAMÁ: Near San Carlos, elev. 0–10 m, 1 m, *Allen 1136* (GH, MO, NY, US). Between Río Pacora & Chepo, roadside savanna, *Porter et al. 5126A* (MO).

6. **Physalis lagascae** R. & S. *in* L., Syst. Veg. 4: 679. 1819. TYPE: Based on *P. parviflora* Lagasca.

P. parviflora Lagasca, Gen. Sp. Diagn. 11. 1816, non Zuccagni *in* Roem., Collect. 130. 1806, nec R. Br., Prodr. 447. 1810. TYPE: (not seen).
P. rydbergii Rusby, Bull. New York Bot. Gard. 4: 423. 1907, non Fern., Proc. Amer. Acad. Arts 35: 569. 1900. TYPE: Bolivia, *Bang 2520* (MO, NY).

Erect or spreading *herb* to 60 cm tall, stems glabrate with scattered, stout, white, often jointed hairs 1–4 mm long, and with minute, appressed or spreading hairs somewhat localized near the nodes. *Leaves* to 5 cm long, mostly half that

size, ovate, sometimes broadly so, apically acuminate, acute or obtuse, basally deltoid, truncate or subcordate, often oblique, the margins entire or sinuate, rarely toothed, glabrate but with minute hairs along the veins and minutely papillate on the lamina; petioles 1–3 cm long; small, 5 mm long, elliptical minor leaves sometimes present. *Pedicels* to 5 mm long, slender with scattered, long, stout white hairs. *Flowers* with the calyx 3–4 mm long, 2.5–3 mm broad at the base of the lobes with scattered, stout, long white hairs, especially along the ribs, the lobes to 1.5 mm long, deltoid; corolla mostly with a contrasting eye, 5–7 mm long, pubescent in the tube; anthers blue or violet, 1–1.5 mm long. *Fruiting calyx* 10-ribbed, the ribs rough or kinky in outline by virtue of enations or teeth produced mostly at the base of the stout hairs, glabrate or pubescent but mostly with some stout white hairs along the calyx ribs, the calyx usually drying reticulate-veined, 10–20 mm long; the berry globose, 6–10 mm across.

No type has been seen for the name used here—the concept is that of Waterfall, 1967), which seems also to be that of Rydberg, Dunal, Nees and other workers. A search for authentic material at Madrid (MA) was unsuccessful. In naming *P. lagascae*, Roemer and Schultes questioned whether this species might be the same as *P. ixocarpa* Brot. *ex* Hornem. or *P. inocarpa* Brot. In a recent study, Fernandes (Bol. Soc. Brot., ser. 2. 49: 343–367. 1970) discussed typification of the first of these names, which does not apply to the Panamanian taxon. Few of Brotero's types are extant, and until authentic material of *P. inocarpa* can be found, the name is best ignored.

Physalis lagascae is best recognized by its small leaves, flowers, and fruits and by the teeth or enations of the calyx ribs which give the angles a kinky appearance. The stout white hairs of the calyx and stems is also a useful character.

This species is ruderal in habitat and is reported as ephemeral or annual in life span. Although there are few collections from Panama, it may be expected almost anywhere in the country where there is agricultural or urban disturbance. It is well adapted to regions with a seasonal dry period.

CANAL ZONE: Chiva Chiva Trail near Miraflores Lake, disturbed area in sun, *Tyson 1386* (DUKE, FSU, MO), *1389* (MO). COCLÉ: 10 mi. E of Natá at Río Grande, infrequent in sun, 2 ft. tall, *Tyson 5254* (DUKE, FSU, MO). PANAMÁ: Savanna near Río Pacora and Chepo Highway, *Duke 5940* (FSU, F, MO).

7. **Physalis minuta** Griggs, Torreya 3: 138–139, 1903. LECTOTYPE: Guerrero, Mexico, *Palmer 304* (US; MO, isolectotype).

Erect or spreading *herb*, glabrate to the naked eye but mostly evenly covered with minute, stiff, perhaps glandular hairs. *Leaves* small, ovate or elliptic, mostly less than 2 cm long, apically acute or obtuse and basally obtuse, the margin serrate; petioles sometimes longer than the leaves. *Flowers* inconspicuous on short, filiform pedicels 3–10 mm long and puberulent with minute antrorse hairs; calyx 2–4 mm long, ca. 1.5 mm across, evenly fine-puberulent, the lobes 1 mm wide at the base and 1–2 mm long; corolla 4–8 mm long, with or without markings in the eye; the filaments stout and unequal; the anthers blue or yellow, 1.3–2.5 mm long, curling somewhat on drying. *Fruit* on slender pedicels, 4–10 mm long,

the fruiting calyx 15–18 mm long, 5-angled, minutely puberulent, the berry ca. 7 mm across.

This species is best recognized by its small leaves, flowers, and fruits, and if a lens is at hand, by the minute pubescence. The leaves may be succulent.

In Panama, *Physalis minuta* has been found only in the section of Los Santos facing the Gulf of Panama. It ranges from Los Santos to Mexico (Colima) and is never many kilometers from the Pacific coast. Some collectors report it from truly coastal sites, and the almost glandular nature of the minute hairs and succulent appearance suggest that it may have some salt tolerance.

Griggs in his original description quotes Palmer, the collector, as saying that the fruits are available in markets of Acapulco year round and are cooked in "soups, gravies and stuffing of fowls." While there is no information of such uses in Panama, the small berries of this species would require tedious collecting and hulling.

LOS SANTOS: Beach at Monagre, herb, prostrate, *Burch et al. 1205* (MO). Las Tablas, *Dwyer 1124* (MO). Monagre Beach 5 mi. SE of Chitré, *Tyson et al. 2892* (MO, SCZ).

8. **Physalis philadelphica** Lam., Encyl. 2: 101. 1786. TYPE: P-Lam.[31]

Erect, short-lived *herb* to 80 cm tall; stems weak although sometimes stout, pilose near the base, glabrate above with minute appressed hairs. *Leaves* to 10 cm long, ovate, apically acuminate, basally obtuse and mostly oblique or dimidiate, the margins dentate or repand, thin and sparingly pubescent with short simple hairs; petioles half as long to as long as the blade. *Pedicels* 3–7 mm long, about equaling the flowering calyces, pilose with spreading hairs. *Flowers* with the calyx 3–8 mm long, relatively broad, lobed about halfway, the lobes deltoid and sometimes caudate, pubescent with short spreading hairs mostly on the angles; corolla with a contrasting eye, 8–15 mm long, sometimes reflexing open to 18 mm across; filaments slender, perhaps unequal, the anthers purple or blue, twisting after anthesis, 2–3 mm long. *Fruits* on recurved pedicels 3–10 mm long, fruiting calyces slightly 5-angled and 10-ribbed, 20–50 cm long with some scattered hairs; berry globose, ca. 10 mm long, oily or viscid, fleshy.

This species is identifiable by its large, broad calyx when in bud, its viscid berry, and by the absence of long hairs on the upper part of the stem. Presence of hairs on the fruiting calyx will separate it from *P. cordata*.

Physalis philadelphica is a species of Mexico and the United States, but it ranges into Canada on the north and into the Antilles. It has been collected from scattered localities in Central America besides Panama. The single Panamanian collection is from a flourishing colony of tall, weak plants. It occurs from ca. 2,000 m elevation down to sea level.

Waterfall (1967) placed *P. ixocarpa* Brot. *ex* Hornem., into synonymy under *P. philadelphica*; but Fernandes has shown that the two species are quite different,

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[31] For synonyms, see Fernandes (Bol. Soc. Brot., ser. 2. 49: 343–367. 1970). Only the above name has been used for Panamanian plants.

P. ixocarpa referring to a plant common in parts of Europe but without known localities in the New World.

CHIRIQUÍ: Above Nueva Suisa, Volcán District, in dense forest shade on path between vegetable fields, *D'Arcy* 5323 (C, COI, G, MO, MPU, P).

9. **Physalis pubescens** L., Sp. Pl. 183. 1753. TYPE: "In India utraque" (LINN 247.11; MO, photos).

9a. **Physalis pubescens** L. var. **pubescens.**

P. hylophila Standl., Jour. Washington Acad. Sci. 14: 243. 1924. TYPE: El Salvador, *Standley 20971* (GH, NY, US).

More or less erect *herb* to 90 cm tall, stems mostly villous with spreading, often viscid hairs, 1–4 mm long, especially below, and with short, sometimes dense hairs on young and upper parts, rarely glabrate, the hairs often oriented in vertical lines or on only one side of the stem. *Leaves* 2–5(–10) cm long; broadly ovate or elliptical, apically acuminate or acute, basally subcordate to shortly cuneate, often slightly oblique, the margins entire, sinuate or toothed, mostly hairy overall and sometimes viscid; petioles mostly shorter than the leaves with erect and spreading hairs. *Pedicels* mostly about equaling the flowering calyx, vestite with erect and spreading hairs. *Flowers* with the calyx 4–6 mm long, 3–10 mm across at the base of the lobes, mostly densely villous with erect or spreading usually glandular hairs, the lobes acute; corolla with a strongly contrasting, pubescent eye, 6–12 mm long; anthers blue, 1.5–3 mm long. *Fruits* on slender pedicels less than half as long as the calyces; fruiting calyx 2–4 cm long, somewhat pubescent, especially along the edges of the ribs, strongly 5-angled and indented at the base; berry globose, 10–18 mm across.

Physalis pubescens may be recognized by its dark eye and anthers, which contrast strongly with the otherwise yellow corolla, by its general hairiness, especially on the lower parts of the stems, and by the strongly 5-angled, usually pubescent calyx.

This species displays wide ecological tolerance; from rain forest to desert scrub and from sand dunes to wet meadows. It is wide ranging, occurring from Panama north to Massachusetts and south to Chile and Argentina and throughout warm parts of the Old World as an introduced weed. In Panama, most collections are from the lowlands, but it ranges to middle if not upper elevations.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 301* (F, US). CANAL ZONE: Road S-11, NW of Escobal, *Croat 12449* (MO). Barro Colorado Island, *Ebinger 594* (US, right hand specimen only). Chagres, *Fendler 248* (GH, MO, US). In government forest along Las Cruces Trail, 75 m, *Hunter & Allen 764* (MO). Madden Forest Preserve along Las Cruces Trail and highway, deep rain forest, *Lewis et al. 5316* (MO). Along trail between Gamboa and Cruces, 50–80 m, *Pittier 3772* (F, US). Vicinity of Madden Dam near Río Chagres, 50–75 m, *Seibert 554* (GH, MO, NY; cited under *P. turbinata* Med. by Waterfall (1967)). Miller Trail, Barro Colorado Island, *Shattuck 45* (F, MO). COCLÉ: 12 mi. NE of Penonomé, granitic river gorge, 1,200 ft, *Lewis et al. 1531* (MO). 10 mi. E of Nata at Río Grande, *Tyson 5292* (FSU, SCZ). COLÓN: Roadside between 5–7 mi. SW of Portobelo towards Maria Chiquita, *Wilbur & Weaver 11205* (DUKE). DARIÉN: Weed along Río Pirre, *D'Arcy 5532* (BIRM, COL, MO, MPU). Village of Manene, *Kirkbride & Bristan 1600* (MO). LOS SANTOS: Vicinity

of headwaters of Río Pedregal, 25 mi. SW of Tonosí, cloud forest and native clearing, 2,500–3,000 ft, *Lewis et al. 2886* (C, MO). PANAMÁ: Vicinity of La Jagua, wet savanna E of Panama City, *Bartlett & Lasser 16379* (MO). Edge of forest, top of ridge N of El Llano, *D'Arcy & D'Arcy 6040* (ADW, C, MO, PMA, UCWI). 5–6 mi. E of Chepo on Pan American Highway, *Duke 4028* (MO). Natural Bridge, near Madden Lake, *Gentry 5608* (ADW, F, MO, VIR). Chimán, clearing in rain forest, *Lewis et al. 3295* (MO, PMA). Gorgona Beach, *Woodson et al. 1694* (F, GH, MO, NY).

9b. **Physalis pubescens** var. **hygrophila** (Mart.) Dun. *in* DC., Prodr. 13(1): 446. 1852.

P. hygrophila Mart., Flora, Beibl. 24(2): 86–7. 1841. TYPE: Brazil, *Martius 624* (MO).

The var. *hygrophila* differs from typical *P. pubescens* principally in the corolla lacking a conspicuous eye. The anthers may be blue or yellow. In specimens examined, including the type, leaves are smaller than many collections of the typical variety but are well within the range displayed by var. *pubescens* in Panama and elsewhere. The var. *hygrophila* is known from scattered collections from Mexico, Panama, and Brazil.

DARIÉN: Vicinity of El Real, 15 m, *Allen 956* (F, MO). 1 mi. N of Río Sabana, *Tyson et al. 4803* (SCZ; the specimen at MO with this number is *P. cordata* Mill.).

17. RAHOWARDIANA

Rahowardiana D'Arcy.[32] TYPE: *R. wardiana* D'Arcy.

Shrub, hemi-epiphytic, unarmed. *Leaves* glabrate, subcoriaceous, opposite or approximate and appearing verticellate at the ends of twigs. *Inflorescence* a crowded, globose, tight panicle, the axes short and crowded, the pedicels stout. *Flowers* showy, the calyx tubular-angulate, shallowly or deeply, irregularly 5-parted, coriaceous; corolla tubular, slightly emerging from the calyx, slightly curved, 5-lobed, the lobes clawed, revolute; stamens 5, inserted near the base of the corolla tube, the filaments slender, the anthers linear-tapering upwards, 2-thecate, opening by longitudinal slits; ovary 5-lobed with an ovule-bearing apicule resembling a thickening of the style base, the carpels 2, many ovuled, the placentae axile, somewhat proliferated, the style slender, included, thickened at the base, the stigma 1–2-lobed. *Fruit* (immature) narrowly conical or sub-cylindrical with a sharp point.

A genus known only from central Panama, *Rahowardiana* shows similarities to *Markea*, *Juanulloa*, and other hemi-epiphytic Solanaceae occurring in the region. The contraction of the ovuliferous portion of the ovary into a style base and the presumed sharp-pointed, narrowly conical fruit are distinctive. The anthers, slender and narrow somewhat as in some species of *Markea*, are evenly attenuate to a pointed apex and more like those in *Juanulloa* (*e.g. Allen* 5289 (MO), Costa Rica).

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[32] *Rahowardiana* D'Arcy, gen. nov. Frutex labruscave, foliis glabratis, subcoriaceis; inflorescentia singulariter, globosa, corollis aliquot emergentibus splendide; ovario apiculo ovulifero gerenti; fructu immaturo elongato, apiculato.

The genus is named for Richard Alden Howard, the Arnold Arboretum, who has encouraged and assisted botanists of many institutions and locales.

1. **Rahowardiana wardiana** D'Arcy.[33] TYPE: Panama, *Wilbur & Luteyn 3150* (DUKE).—FIG. 16.

Shrub, epiphytic or ?hemiepiphytic, 2 m tall; twigs stout, irregularly angled, the bark flaking in chartaceous, shiny wafers, apically angled. *Leaves* to ca. 15 cm long, obovate, apically short acuminate, basally obtuse, entire, subcoriaceous, glabrous on the lamina, the veins 4–5 on each side of the prominent midvein, minor venation obscure above, drying elevated beneath, the major veins minutely hispid beneath; petioles stout, almost wanting or to 15 cm long, channelled above, the leaves alternate and aggregated into 3–4-leaf verticels. *Inflorescence* a large, dense globose panicle 7–15 cm across, the pedicels drying brown, 8–15 mm long, slender, prominently tuberculate, a few flowers opening at a time. *Flowers* with the calyx tubular, strongly angled, dark purple, abruptly rounded basally, 3–4 cm long, apically 5-toothed, the sinuses splitting a short distance or nearly to the base; corolla yellow, ca. 3 mm long, slightly exserted, tubular, slightly curved, somewhat 5-angled, narrower in the upper half, 5-lobed, the lobes recurved with a prominent, narrow claw running perpendicular to the floral axis; stamens equal, the filaments glabrous, slender, inserted at the base of the corolla tube, the anthers narrow, almost linear, tapering slightly to the apex, apiculate, 2-locular, dehiscing longitudinally and the theca walls folding back to back, 8–9 mm long, included; ovary sessile, 5 lobed, contracted sharply above into a 2-lobed style base, 2-carpellate, the placentae somewhat proliferated and running into the stylar base area, the ovules slender, cylindrical but curved through 15–25°, the style slender, glabrous, the stigma small, indistinctly 2-lobed, included. *Fruit* not seen but immature fruits reaching the level of the calyx tips were narrowly conical with slender, elongate apices.

This species is singular in appearance, the inflorescence consisting of a purplish-brown ball ca. 10 cm across with scattered, bright yellow corollas emerging here and there. The leaves resemble those of *Markea ulei* or *M. neurantha* but are thicker and sturdier and have minute erect hairs along the major veins beneath.

The species was spotted in the field by James L. Luteyn of Duke University who very kindly supplied the author with a photograph and pickled flowering material as well as a good set of herbarium specimens. Duplicates will presumably be distributed by Duke University.

Rahowardiana wardiana is named for Daniel Bertram Ward, Professor of Botany, University of Florida.

COCLÉ: Beyond La Mesa towards Los Llano and the Panamá/Coclé border N of El Valle de Antón, 800–860 m, *Luteyn 3150* (DUKE). Trailside woods near La Mesa ca. 5 mi. N of El Valle, *Wilbur & Luteyn 11723* (DUKE).

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[33] *Rahowardiana wardiana* D'Arcy, sp. nov. Frutex, foliis obovatis, subcoriaceis; inflorescentia globosa purpurea, calyce tubuloso, corolla tubulosa, aurea, lobis recurvata; fructu non vidi.

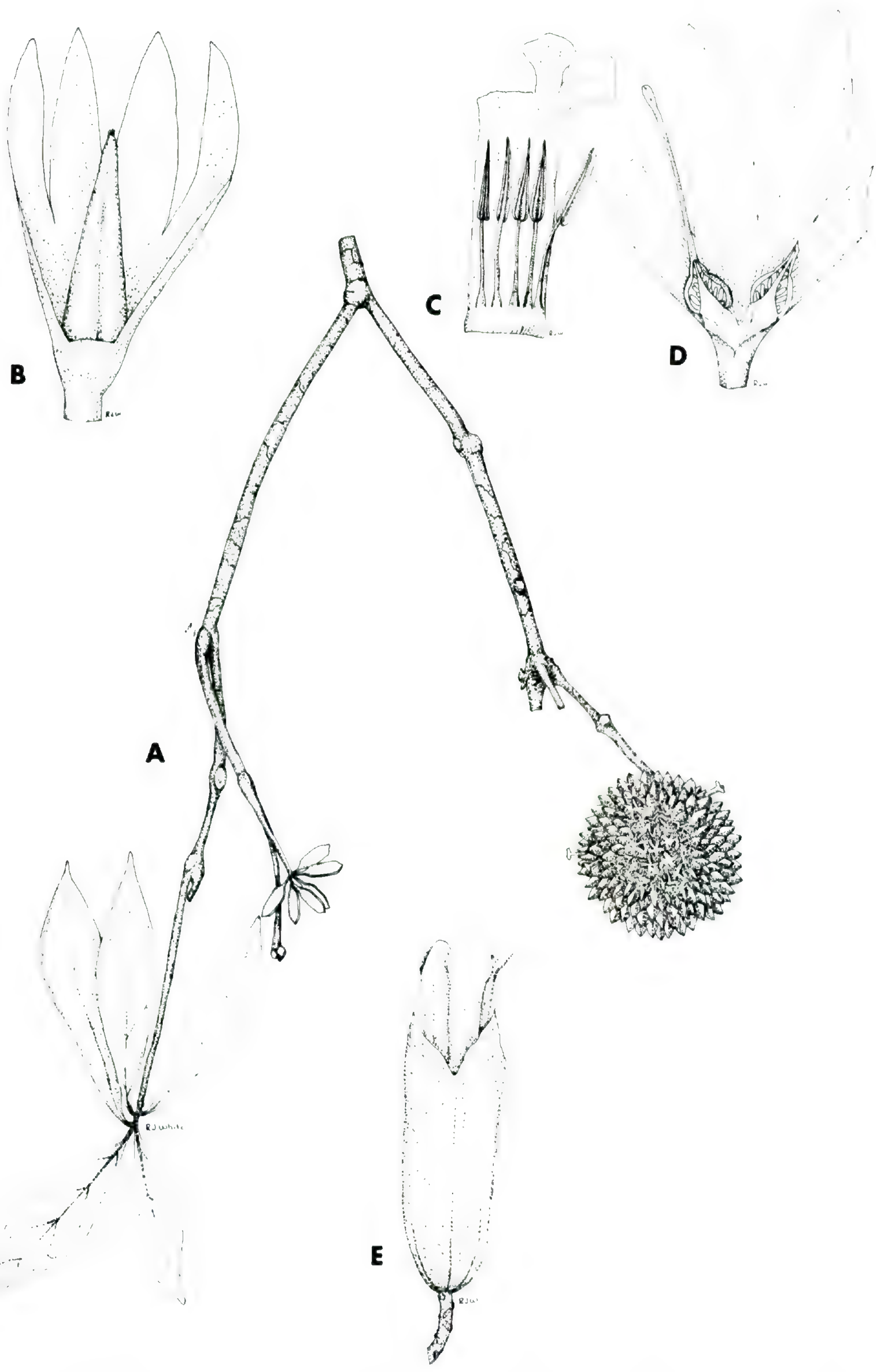

FIGURE 16. *Rahowardiana wardiana* D'Arcy.—A. Flowering branch (× ¼).—B. Young fruit, the calyx partly removed (× 1½).—C. Androecium, the corolla partly removed (× 1½).—D. Ovary cut open, corolla and part of calyx removed (× 2).—E. Single flower (× 2½). [After *Luteyn 3150* (DUKE).]

18. SCHWENCKIA

Schwenckia L., Gen. Pl., ed. 4: 577 [567]. 1764, "*Schwenkia*" sphalma auctorum. TYPE: *S. americana* L.

Chaetochilus Vahl, Enum. Pl. 1: 101. 1894. TYPE: *C. lateriflorus* Vahl.
Matthissonia Raddi, Mem. Mat. Fis. Soc. Ital. Soc. Ital. Sci. 18: 1820. TYPE: *M. paniculata* Raddi.
Mathaea Vell., Fl. Flum. 22. 1825. TYPE: *M. apostolica* Vell.

Erect *herbs* or *subshrubs*, unarmed, glabrous or pubescent. *Leaves* simple, entire, alternate or fascicled. *Inflorescence* terminal, flowers small, solitary or in lax panicles; calyx tubular or campanulate, valvate in bud, 5-dentate or -lobed; corolla narrowly tubular, sometimes saccate, often with a slight enlargement in the upper portion at the level of the anthers, apically with 5 short, deltoid to acicular, sometimes emarginate lobes and sometimes 5 slender appendages alternating with them; stamens 4 or 2 with 0–3 staminodes, the filaments inserted at the middle of the tube, sometimes flattened, sometimes basally pubescent, the anthers included, coherent or connate; ovary on a hypogynous cupular disc, 2-loculed, several- to many-seeded. *Fruit* a dry, many-seeded, longitudinally dehiscent capsule, smaller or larger than the calyx; seeds minute, smooth or rugose, sometimes flattened on one side.

A genus reportedly including 25 species of Central and South America and the Antilles. One species, the one treated here, is also widespread in Africa. There are no known uses and to judge from the number of specimens in North American herbaria, the plants are seldom collected. The plants are small with small flowers, which may account for the paucity of collections. The reduced stamen number has led to placement of the genus in the Salpiglossidae along with *Brunfelsia* and *Browallia*.

Schwenckia is named for Martin Wilhelm Schwencke, 1707–1785, a physician and botanist at The Hague. For a discussion of orthography of the generic name see Heine (Kew Bull. 16: 465. 1963).

1. **Schwenckia americana** Royen *ex* L., Gen. Pl., ed 4. 577 [567]. 1764. TYPE: (not seen).—FIG. 17.

Ascending *herb*, branched near the base to 70 cm tall; stems puberulent with antrorse curved hairs, leafy on the basal half. *Leaves* ovate, elliptic, obovate or rhombic, mostly 2 cm long and 7 mm broad, apically acute or obtuse, basally narrowed to the short, 2 mm petiole, pubescent and the midvein prominent on both sides, veins ca. 3 on each side. *Inflorescence* a scapose, open panicle, elongate, the stem leaves declining in size upward to become minute bracts near the apex; peduncles solitary, slender, to 24 cm long; pedicels solitary, 2–3 mm long, in fruit slightly longer with an articulation near the base. *Flowers* small, with the calyx tubular, 3 mm long, 4–5 lobed to about ⅓ the way down, strongly nerved, sparingly pubescent inside and out; corolla 10–12 mm long, narrowly tubular, glabrous outside, pubescent on the lower ⅓ inside, strongly nerved, minutely 5-lobed, the lobes deltoid and sometimes unequal, the nerves terminating in 2–5, linear-spatulate, equal or unequal glandular appendages which may

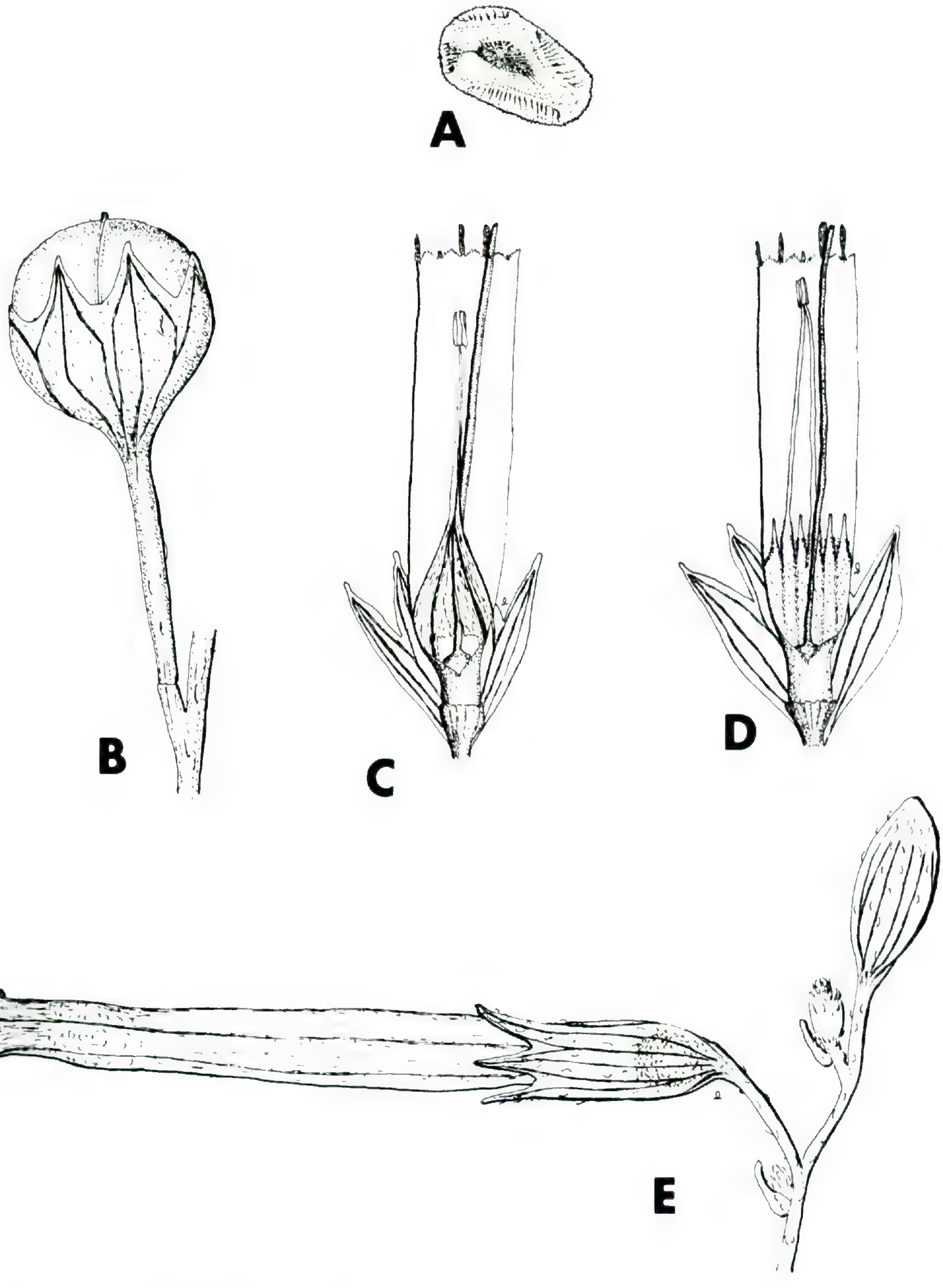

FIGURE 17. *Schwenckia americana* L.—A. Seed (× 3⅕).—B. Capsule (× 8).—C. Flower, portion of corolla removed to show filaments converging over the ovary (× 5⅗).—D. Flower, the corolla and filaments opened to show insertion of stamens (× 5⅗).—E. Twig with flower and buds (× 8). [After *Allen* 826 (US).]

slightly exceed the corolla lobes; stamens 2, equal, the filaments inserted about ⅓ the way up the corolla tube, pubescent on the lower ½ (including adnate portion), tape-like below, tapering just above the point of insertion, anthers connate, oblong, 1 mm long, dehiscing longitudinally, staminodes 3, equal, consisting of filaments which resemble those of the stamens for the adnate portion, tapering to an apex 1 mm above the point of insertion, the filaments of stamens and staminodes coherent by marginal hairs to form a closed cone over the ovary; ovary ellipsoidal, 2 mm long, constricted around the middle, the style straight, the stigma punctiform, exserted as long as the longest corolla appendage. *Fruit* a globose capsule with a small but manifest apicule, dehiscent by a single, elevated suture which transverses the apex, and sometimes (on herbarium sheets) by other longitudinal slits; seed 0.6 mm long, a pyramidal frustum, ferrugineous, minutely striate with tuberculae in rows.

Only two collections of this species have been seen from Panama. There are more collections from Costa Rica and other Central American countries, but the species is apparently rare.

COCLÉ: Natá, ca. 50 m, *Allen 826* (F, MO, NY, US). Llanos, Penonomé, *Ebinger 994* (US). Aguadulce in savannas near sea level, *Pittier 4880* (NY, US).

19. SOLANDRA

Solandra Sw., Vet.-Akad. Stockholm Nya. Handl. 8: 300. 1787, nom. cons. against *Solandra* L., Umbelliferae. TYPE: *S. grandiflora* Sw.

Swartzia J. F. Gmel., Syst. 360. 1791. TYPE: *Solandra grandiflora* Sw.

Scandent *shrubs*, high-climbing *hemi-epiphytes* or large stemmed *lianas*, unarmed; stems mostly glabrous, stout, to 5 cm across, with no apparent pith, the bark flaking; twigs stout with a large pith. *Leaves* simple, entire, membranaceous, coriaceous or somewhat succulent, glabrous or variously pubescent with simple or dendritic hairs, sometimes with minute glandular trichomes or excrescences; minor leaves mostly wanting. *Inflorescence* a 1- or few-flowered cluster at the ends of twigs or short shoots, pedicels stout, rarely elongate, leaving an expanded cicatrix on the twig. *Flowers* with the calyces mostly tubular, but sometimes ellipsoidal or campanulate, angled and sometimes inflated, splitting in flower into 2–5 irregular lobes, splitting almost to the base in fruit, pubescent or not; corolla imbricate and the apex flattened or broadly rounded in bud, often very large, fleshy and mostly glabrous, campanulate, craterform or funnelform, often slightly zygomorphic, the lobes entire to fimbriate and often recurved; stamens 5, equal (unequal in bud)[34] mostly exserted, filaments inserted at the base of the tube, often pubescent at the point of insertion, straight or gently curved in the upper portion; anthers fabiform, 4-loculed, not apiculate, dehiscing longitudinally and the thecae walls reversing 90° to become elliptical, ovary conical, sometimes apically flattened, partly or mostly immersed in the receptacle, and thus partly inferior and in a perigynous disc or nectary, 4-loculed, perhaps becoming partly 2-loculed, ovules many, the style sometimes much exceeding the anthers and

[34] Details are amplified in the description of *S. brachycalyx*.

persistent for a time on the fruit. *Fruit* a leathery berry, loosely enclosed by the ruptured calyx; seeds many, reniform.

A genus of perhaps eight species ranging from Mexico and the Antilles to Brazil. Some species are commonly cultivated for ornament in tropical gardens and temperate greenhouses. The flowers are mostly showy, and some are very fragrant. In Mexico and perhaps other countries species of *Solandra* possessed ancient medicinal or narcotic repute. Fruits of some species are comestible.

Solandra is closely related to *Markea* sect. *Megalandra*, and the distinctions are not well understood. Both have coriaceous leaves, and the corolla shape is similar. In both groups the flowers are perigynous. However, these species of *Markea* have punctate dots on the leaf undersides, and in most of them the anthers are elongate. The ovaries are 2-loculed and not 4-loculed as in *Solandra*. Superficially, *Solandra* is similar to several other genera of Solanaceae and has been confused with *Datura*. The perigynous flower with imbricate corolla lobes and the usually elliptical form of the dehisced anthers are distinctive, while for most species the shape of the large showy flowers is diagnostic. The 4-loculed ovary is suggestive of *Datura*, but the relationship may be remote. Superficially similar species of *Brugmansia* have 2-loculed ovaries.

Although plentiful in some countries and commonly available in tropical nurseries, *Solandra* species are poorly represented in herbaria, and a number of collections consist of fallen flowers only. In many cases, herbarium material is not adequate for species determination.

In the Cerro Punta region of Chiriquí, large vines of *Solandra* are particularly common, and along streamsides many of the large-buttressed trees support *Solandra* plants growing well out of reach from the ground. Cultivation of these plants is not so frequent in Panama as might be expected for such an attractive plant.

"Floripondio del monte" (Mexico), "copa de oro" (Mexico), "chalice vine," "cup of gold" (English).

Solandra is named for Daniel C. Solander, 1736–86, Swedish, a student of Linnaeus who accompanied Captain Cook on his first voyage (1768–71).

Useful reference:

Martinez, M. Las *Solandras* de México, con una especie nueva. Anales Inst. Biol. Univ. Nac. México 37: 97–106. 1966.

a. Leaves glabrous.
  b. Anthers more than 10 mm long[35] ..... 3. *S. maxima*
  bb. Anthers less than 9 mm long ..... 2. *S. grandiflora*
aa. Leaves with hairs in the vein axils and along the midvein on the leaf undersides, otherwise glabrous ..... 1. *S. brachycalyx*

1. **Solandra brachycalyx** O. Kuntze, Rev. Gen. Pl. 2: 453. 1891. LECTOTYPE: Costa Rica, *Hoffman 94* (B, not seen; MO, photo).—FIG. 18.

Large *hemi-epiphyte* extending from 7–30 m high in large trees, stems ca. 5 cm thick near the ground, mostly terete, spongy, without demarcated pith, the

[35] Peter S. Green, Kew, must be credited with pointing out the taxonomic significance of anther size.

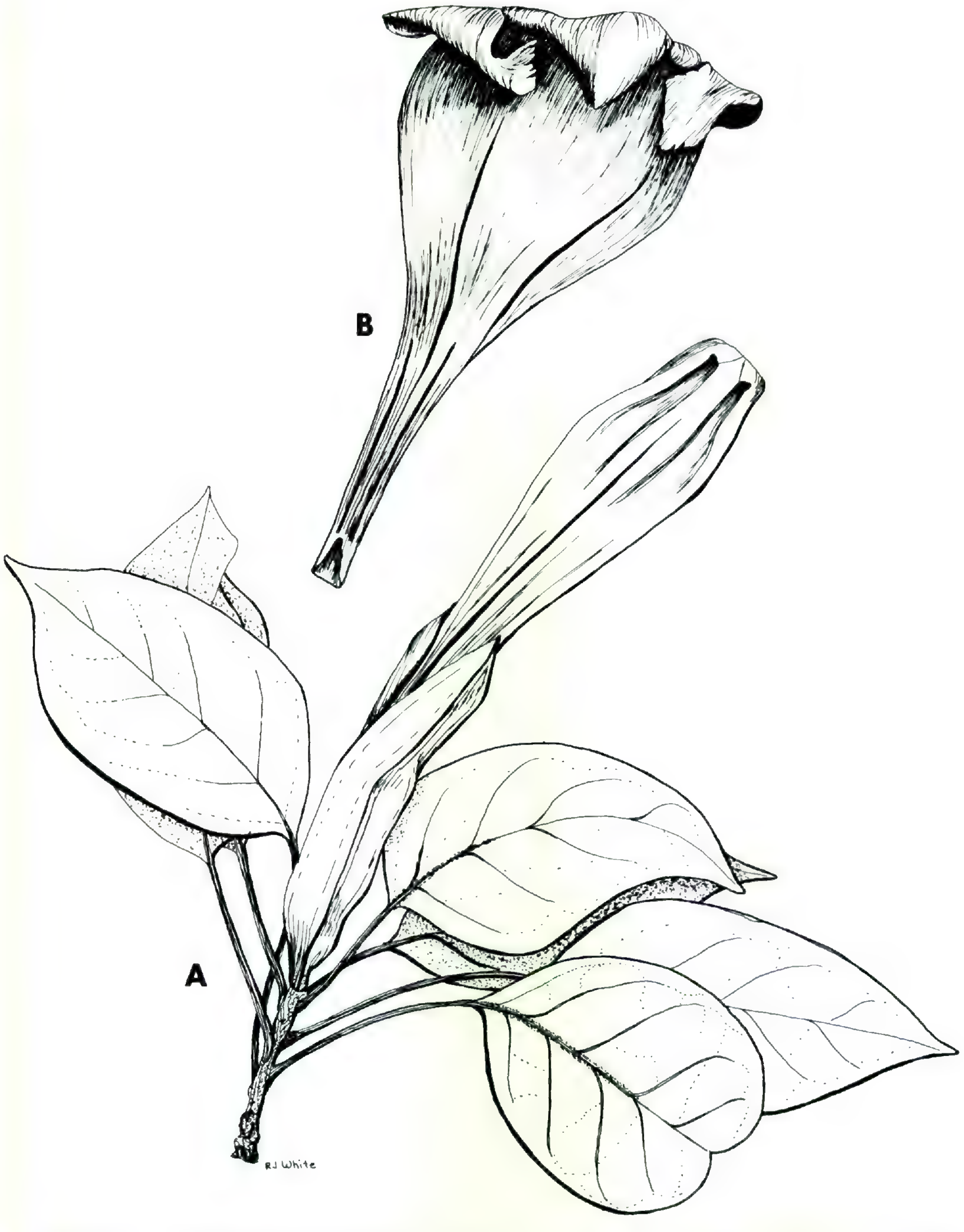

FIGURE 18. *Solandra brachycalyx* O. Kuntze.—A. Twig with bud (× ½).—B. Corolla (× ½). [After *D'Arcy 5340* (MO).]

old bark flaking in rectangles, young bark silvery brown; twigs stout, ca. 8 mm thick with a large pith and reticulate corky markings, the leaves and flowers on short shoots with an elongate cicatrix. *Leaves* ca. 11 cm long, broadly elliptical-ovate, apically short acuminate, basally obtuse or acuminate, often slightly oblique, slightly coriaceous or somewhat succulent, glabrous except for

rows of dense, conspicuous, whitish (drying brownish) hairs along the basal portion of the midrib beneath and some hairs on the lateral veins, veins ca. 5 on each side of the midvein, the midvein slightly recurved; petioles slender, 4–6 cm long, glabrous, channeled above near the leaf, terete below. *Pedicels* glabrous, short and stout, 1–1.5 cm thick and about as long, broadening into the calyx and hardly distinct from it, with many light green round tubercules which extend up onto the calyx where they become elongate. *Flowers* with the calyx green, glabrous, mostly 8 cm long, tubular with five prominent angles extending to near the base, fleshy, splitting along 3 angles to about ⅓ the way down, perhaps further in fruit, the tips of the lobes obtuse and slightly mucronate; the corolla 15–25 cm long, craterform, fleshy, greenish-white and yellow, almost orange with age, outside with 5 strong, green, slightly sunken ribs on the tube and limb, inside with 5 large purple guide lines in the limb alternating with 5 smaller, fading guide lines, glabrous outside, glabrous inside except for conspicuous lanate tufts 5–10 mm below the point of anther insertion, the tube slender, 5–7 cm long, the limb 6–8 cm long and 5–5.6 cm across, the lobes rotund-emarginate, ca. 3 cm long, the margins laciniate; filaments slightly geniculate at point of insertion, pubescent just below, the anthers fabiform, brown, 10–12 mm long and 5 mm across (after dehiscence); ovary glabrous, apically concave at the apex, 4-loculed with no sign of obliqueness relative to the floral axis, style exserted, becoming elongate, to 25 (or more?) cm long, slender, greenish white, the stigma capitate. *Fruit* not seen.

Solandra brachycalyx is best recognized by the pubescence along the midvein on the leaf undersides (the leaf is otherwise glabrous), and by the anthers, 11 mm long. The showy flowers of this species show less tendency to dry brownish than some other species in the genus. In bud the anthers are clearly tridynamous, the bottom two long, the lateral two short and the fifth (upper) reduced. This is not apparent in the opened flower. Most flowers are attacked at an early stage and the interior of the ovary eaten out, leaving one large, dirty locule.

Solandra brachycalyx is known in Panama only from the Chiriquí mountains where it is plentiful at upper elevations. Specimens have also been seen from Costa Rica and Guatemala.

CHIRIQUÍ: Bajo Mono-Robalo Trail, W slopes of Cerro Horqueta, 5,000–7,000 ft, *Allen 4777* (MO). Nueva Suisa, 5,500 ft, *D'Arcy 5338* (MO). Bambito, Volcán District, 5,000 ft, *D'Arcy 5340* (K, MO, MPU). Nueva Suisa, Volcán District, *D'Arcy 5415* (MO). Cerro Horqueta, 1,500 m, *Duke et al. 13625* (MO). Cerro Horqueta, cloud forest, 6,500 ft, *von Hagen & von Hagen 2105* (MO).

2. **Solandra grandiflora** Sw., Kongl. Vet. Acad. Handl. 8: 300–306, *Tab. 11.* 1787. TYPE: Jamaica, *Swartz, s.n.* (?S, not seen).

High climbing *hemi-epiphyte* or cultivated *shrub* to 1.5 m tall. *Leaves* broadly elliptical, coriaceous, often drying shiny, mostly obtuse at each end or short acuminate apically, glabrous, petioles slender, 3–5 cm long. *Pedicels* stout, sometimes tuberculate. *Flowers* showy, the calyx tubular or campanulate, 4–9 cm long, angled and inflated, appearing slender or stout when dried, splitting ¼–¾ the way down into 3–5 lobes, the lobes slender or broad, mostly apiculate,

glabrous outside, somewhat succulent; the corolla fleshy, craterform, yellow or golden colored, becoming orange-brown with age, 5 purplish ribs mostly present within, the tube slender, 7–15 mm long and included or partly exserted from the calyx, abruptly expanded into a large limb (cup), 6–12 cm in diameter, the lobes rotund, entire to erose margined, glabrous outside, pilose for a distance below the point of filament insertion; filaments straight or slightly geniculate at the point of insertion, glabrous, the anthers 6–8(–9) mm long; ovary mostly inferior in flower. *Fruit* not seen.

This species is similar to *S. maxima* (Sessé & Moc.) P. S. Green, which has a generally longer corolla tube and longer anthers, and to *S. longiflora* Tussac of Cuba, which has a much longer corolla tube and anthers only 5–7 mm long. The corolla tube is generally more pubescent within in specimens of *S. grandiflora* from Central America than in those from Jamaica.

Solandra grandiflora is a favorite ornamental in tropical gardens, and is usually grown as a specimen shrub or fence covering rather than as a high climber. It is less commonly grown in Panama than in some other tropical countries.

CANAL ZONE: Albrook Air Force Base near Visiting Officers' Quarters, *Lewis et al. 2255* (MO). COCLÉ: Near El Valle, 600–1,000 m, woody liana in tops of large trees; *Allen 1212* (US, GH, MO). Region N of El Valle de Antón, 1,000 m, woody branching liana growing in tops of trees, *Allen 3737* (MO). PANAMÁ: Bald savanna-like areas along road toward top of Cerro Campana, *Duke 5985* (GH, MO). PROVINCE UNKNOWN: Río Cristal, growing on house, *Bouché*, 1954 (MO).

3. **Solandra maxima** (Sessé & Moc.) P. S. Green, Bot. Mag. 176: *Tab. 506.* 1967.

Datura maxima Sessé & Moc., Pl. Nov. Hisp. (in Naturaleza (Mexico City), ser. 2. 1: app.) 25. 1887 [1888]. TYPE: Mexico, *Sessé* (BM).
Solandra nitida auct., non Zucc. *in* Roem., Coll. 128–9. 1809 [1806].

High climbing *hemi-epiphyte* or cultivated as a scandent *shrub* to 1.5 m tall. *Leaves* broadly elliptic, to 14 cm long, apically acuminate, basally mostly obtuse, glabrous or with an occasional hair on the veins beneath; petioles slender, 2–5 cm long. *Flowers* solitary or several in a cluster, each terminal on a short stout peduncle; pedicels stout, 1–1.5 cm long, often with conspicuous tubercules; calyx tubular, 5–8 cm long, angled and sometimes inflated, appearing stout when dried, splitting ¼–⅓ the way down into 3–5 lobes, the lobes slender or broad, apiculate, glabrous outside, sometimes fleshy; corolla fleshy, craterform, conspicuous, yellow, becoming darker with age, 5 conspicuous greenish ribs outside and 5 or 10 purplish ribs within in the tube and limb, the tube slender, 8–13 cm long, mostly abruptly expanded into a large limb (cup) 8–15 cm in diameter, the lobes rotund, crenate to entire margined, glabrous outside, pilose inside for a distance below the point of filament insertion; filaments geniculate at the point of insertion, glabrous, anthers 10–13 cm long; ovary mostly inferior in flower, the superior portion meniscoid, depressed in the center, the style sometimes purplish apically, the stigma green. *Fruit* (Martinez, 1966) ovoid, smooth, shiny, ca. 7 cm across, the calyx persistent.

This species is similar to S. *brachycalyx* from which it differs in its glabrous leaves, the less dissected margins of the corolla lobes and in the usually brown color of the aged corolla. The pubescence in the corolla tube is not as dense or congested as that of S. *brachycalyx*. *Solandra maxima* differs from S. *grandiflora* in its larger anthers.

CHIRIQUÍ: High climbing, pasture above Boquete, 5,200 ft, *D'Arcy 5462* (MO). On river, Río Chiriquí Viejo valley, *White 166* (MO). Bajo Mona, mouth of Quebrada Chiquero along Río Caldera, 1,500–2,000 m, *Woodson et al. 994* (A, MO).

20. SOLANUM

Solanum L. Sp. Pl. 184–188. 1753; Gen. Pl., ed. 5. 85. 1754. TYPE: *S. nigrum* L.

Melongena Mill., Gard. Dict., ed. 4, abr. 1754. TYPE: Not designated.
Aquartia Jacq., Enum. Pl. Carib. 1: 12. 1760. LECTOTYPE: *A. aculeata* Jacq. (= *Solanum aculeatum* (Jacq.) Dun.).
Battata Hill, Veg. Syst. 9: 32. Ca. 1765. TYPE: *Solanum tuberosum* L.
Bassovia Aubl., Pl. Guian. Fr. 1: 217, *tab.* 85. 1775. TYPE: *B. sylvatica* Aubl. (= *Solanum* sp.).
Psolanum Neck., Elem. 2: 60. 1790, nomen nudum.
Dulcamara Moench, Meth. Pl. 514. 1794. TYPE: *D. flexuosa* Moench (= *Solanum dulcamara* L.).
Pseudocapsicum Moench, Meth. Pl. 476. 1794. LECTOTYPE: *P. undulatifolium* Moench (= *S. pseudocapsicum* L.).
Nycterium Vent., Jard. Malmaison *tab.* 85. 1803. TYPE: *N. cordifolium* Vent. (= *S. vespertillio* Ait.).
Androcera Nutt., Gen. N. Amer. Pl. 1: 129. 1818. TYPE: *A. lobata* Nutt. (= *Solanum rostratum* Dun.).
Ceranthera Raf., Amer. Monthly Mag. & Crit. Rev. 176. 1818. TYPE: *C. heteranthera* Raf. (= *Solanum rostratum* Dun.).
Diamonon Raf., Fl. Tell. 2: 76. 1836. TYPE: *D. coriaceum* Raf. (= *Solanum havanense* Jacq., fide O. E. Schulz *in* Urb. Symb. Antill. 6: 1909–10.).
Antimion Raf., Autikon Bot. 109. 1840. TYPE: *A. tomentosum* Raf. (= ?*Solanum* sp.).
Artorhiza Raf., Autikon Bot. 138. 1840, provisional name for *Parmentiera* Raf., non DC.
Parmentiera Raf., Autikon Bot. 108–109. 1840, non DC., Bibl. Univ. Genève 17: 135. 1838, Bignoniaceae. LECTOTYPE: *P. edulis* Raf. (= *Solanum tuberosum* L.).
Scubulon Raf., Autikon Bot. 109. 1840. LECTOTYPE: *S. incanum* Raf. (= ?*Solanum* or *Lycopersicon* sp.).
Cliocarpus Miers, Ann. Mag. Nat. Hist., ser. 2. 4: 141. 1849. TYPE: *C. gardneri* Miers (= *Solanum* sp., sect. *Brevantherum*).
Normania Lowe, Man. Fl. Madagascar 2: 70. 1868. TYPE: *N. triphylla* Lowe (= *Solanum trisectum* Dun.).
Solanopsis Börner, Abh. Naturwiss. Vereine Bremen 21: 282. 1913. TYPE: Based on *S. tuberosum* L.

Herbs, *shrubs*, *trees*, *lianas*, rarely epiphytic or paludal, armed or not, glabrous or pubescent with a variety of simple, branched, stellate, peltate hairs,[4] these often glandular, sometimes accompanied by bristles; some species procumbent or root-climbing, sarmentose, or tuber-bearing. *Leaves* simple or compound, entire, toothed or variously lobed, sometimes armed; petiolate or sessile, sometimes clasping the stem; often in a paired arrangement with one smaller (minor) and the other larger (major), and minor leaves sometimes present at dichotomies of the stem; exstipulate, but the minor leaves sometimes pseudostipular. *Inflorescence* terminal, axillary, opposite the leaves or lateral on the stem, often positioned by concaulescence with the stem, consisting of terminal cincinni which are sometimes curling (scorpioid), elongate (racemose) or contracted (umbellate) and inserted on a peduncle which may be branched (paniculate), very

short (fascicled), or simple (racemose), rarely consisting of a solitary flower on the stem, ebracteate and ebracteolate, pedicels often with articulation above the base perhaps indicating ancestral bracteoles. *Flowers* mostly perfect, rarely dioeceous or monoeceous, not uncommonly with developmental polygamy, (4–)5(–6)-merous, sometimes zygomorphic; calyx mostly manifestly lobed, each lobe vascularized by a trace distinct from the base of the pedicel, mostly splitting at the sinuses during egress of flower or fruit, sometimes accrescent in fruit and loosely or tightly investing the berry; corolla rotate with a very short tube, deeply or shallowly lobed; stamens equal or not, the filaments inserted on the corolla tube, often partially connate, rarely wanting, sometimes pubescent, the anthers basifixed or nearly so, opening by 2 terminal pores and sometimes ultimately longitudinally, dehiscence introrse or extrorse, rarely pubescent, mostly connivant into a tube but rarely connate, the connective small; ovary 2-loculed with proliferation of the placenta, the ovules many, the style (pistillate) equalling or exceeding the anthers, rarely persistent, the stigma small, 2–4-lobed. *Fruit* a juicy, mucilaginous, fleshy, woody or dry berry, sometimes partly hollow, mostly falling from the receptacle, mostly flattened but sometimes prismatic or almost spheroidal, the embryo circinnate around the periphery of the seed, the endosperm fleshy.

The genus may be recognized by the 5-parted calyx and by the anthers which dehisce by terminal pores and lack an expanded connective. Other useful characters for recognition are the rotate, 5-lobed corolla, berry fruit, flattened seeds, stellate pubescence, spines, minor leaves and pedicel scars on the peduncle in species where these features occur.

One of the largest genera of flowering plants, *Solanum* includes over 1,400 described species. Almost world-wide in distribution, the genus has the greatest number of species in tropical America, but there are many species in temperate America and in Africa. The genus is best known for the cultivated potato (*S. tuberosum*), for its many weeds of disturbed habitats, and for the species of upland forests, semi-deserts, coastal and riparian habitats. Distribution is mainly by birds, but other vectors are probably important for some species.

Phylogeny within the genus is undecided. Dunal (1852), Bitter (1911–23), Seithe (1962), D'Arcy (1972) and other workers have tried to recognize a fundamental dichotomy in the genus separating species with stellate hairs, tapering anthers, and spines from those species with simple hairs, stout anthers, and no spines. This simplistic approach has led to disagreement over placement of several major groups.

Elongate ovaries, axillary inflorescences, and clasping petioles may be primitive morphological features in the genus; they appear in the genus *Cyphomandra* and the tribe Daturae. From an ancestral group of plants with primitive morphology, not two but several lines of speciation have emerged. Sections *Archaesolanum* (not in Panama), *Pteroidea*, *Brevantherum*, and perhaps *Aculeigerum* have members with suggestions of primitive morphology, and they are here considered to form parts of a separate subgenera in recognition of separate evolutionary pathways. Reflecting advancement over a primitive *Solanum*

morphology, the subgenera *Solanum* and *Leptostemonum* are morphologically distinctive and may have evolved not as lines of speciation directly from ancestors with primitive morphology, but from plants which would today be placed in one of the other subgenera. Section *Lepidota* may also represent this situation, for while it is placed in subgenus *Brevantherum*, its scutellate hairs and irregularly dehiscent calyx are evolutionary advances over other members of the genus.

Plants of the genus *Solanum* have a very important relationship with man. Many are noxious weeds, and many are important food plants, while others are used for ornamental or medicinal purposes. In terms of acreage, tonnage production, market value, and dietary importance, *Solanum tuberosum* is one of man's most important dicotyledonous crop plants. *Solanum melongena* is an important vegetable crop in some parts of the world. Many other species are of minor or local importance as food plants, *e.g. S. quitoënse* in Panama. *Solanum wendlandii*, *S. seaforthianum*, *S. pseudocapsicum*, and other species are widely grown for ornament. In eastern Europe, *S. torvum* or its relatives provide steroid alkaloids, and many species are used as household remedies in various parts of the world. No species are of known importance for their lumber or fibres.

Useful references:

Bitter, G. [Series of many papers appearing in Fedde Repert. 10–19 and in Bor. Jahrb. Syst. 54–55. For a full bibliography see C. A. Weber, Ber. Deutsche Bot. Ges. 46 (Generalvers. Heft 1): 148–156. 1928.] 1911–1923.

D'Arcy, W. G. Solanaceae studies II: Typification of subdivisions of *Solanum*. Ann. Missouri Bot. Gard. 59: 262–278. 1972 [1973].

Dunal, M. F. Solanaceae. *In* A. P. De Candolle, "Prodromus systematis naturalis regni vegetabilis." 13(1): 1–690. Paris 1852.

Seithe, A. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. Bot. Jahrb. Syst. 81: 261–336. 1962.

a. Plants often spiny; mostly with branches or stellate hairs, if glabrous or with simple hairs then plants spiny.
  b. Anthers tapering, decidedly smaller at the apex than at the base, terminal pores minute; stems or other parts mostly spiny; leaves often lobed (subgenus *Leptostemonum* p. 684).
    c. Lianas, climbing with recurved spines on stem and leaves.
      d. Corolla shallowly lobed, plants glabrous or nearly so ..... A. sect. *Aculeigerum* p. 684
      dd. Corolla deeply lobed, plants manifestly stellate-pubescent.
        e. Leaves petiolate ..... C. sect. *Micracantha* p. 687
        ee. Leaves essentially sessile ..... B. sect. *Eriophylla* p. 685
    cc. Shrubs, trees or perennial herbs, (spines strongly recurved only in sect. *Eriophylla*).
      f. Fruits pubescent, at least until nearly full size .... D. sect. *Lasiocarpa* p. 691
      ff. Fruits glabrous before attaining half size.
        g. Plants with mostly stellate hairs; mostly trees or shrubs.
          h. Leaves petiolate ..... E. sect. *Melongena* p. 698
          hh. Leaves essentially sessile ..... B. sect. *Eriophylla* p. 685
        gg. Plants with mostly simple hairs, especially on the stem; herbs ..... F. sect. *Acanthophora* p. 709
  bb. Anthers not tapering, not much smaller at the apex than at the base; terminal pores relatively large; spines wanting (note trunks of trees); leaves nearly entire (subgenus *Brevantherum* p. 713).

h. Pedicels exceeding the peduncles.
  i. Twigs and leaves with copious stellate hairs (all radii coming off at one point); native species ---- J. sect. *Extensum* p. 722
  ii. Twigs and leaves puberulent with simple or branched hairs (radii not coming off at one point); cultivated species -- G. sect. *Pseudo-capsica* p. 713
hh. Peduncles exceeding the pedicels.
  j. Hairs stellate (all radii coming off at one point).
    k. Inflorescence soon leaf-opposed, mostly less than 5 cm long; leaves contrasting whitish-tomentose beneath ---- J. sect. *Extensum* p. 722
    kk. Inflorescence tardily leaf-opposed if at all, mostly more than 5 cm long; leaves not whitish tomentose beneath ---- I. sect. *Brevantherum* p. 716
  jj. Hairs branched (radii not coming off at one point) or scutellate (radii fused into a peltate disc) and the leaf surface siny-smooth.
    l. Hairs branched; leaves not contrasting above and beneath ---- K. sect. *Holophylla* p. 726
    ll. Hairs scutellate; leaves contrasting above and beneath ---- H. sect. *Lepidota* p. 714
aa. Plants unarmed; plants with simple hairs, a few species with some branched or stellate hairs as well.
  m. Ovaries and fruits elongate-conical; petioles slightly clasping; herbs or trailers (subgenus *Bassovia* p. 729).
    n. Leaves and inflorescences inserted opposite adventitious roots, plants procumbent; leaves trifoliolate ---- L. sect. *Herpystichum* p. 729
    nn. Inflorescence axillary or at a dichotomy of the stem; erect herbs; leaves simple or pinnate, seldom trifoliolate ---- M. sect. *Pteroidea* p. 730
  mm. Ovaries short, fruits globose or ellipsoid; petioles not clasping; habit various.
    o. Plants procumbent; leaves short-petiolate, appearing distichous; inflorescences few-flowered; flowers pinkish ---- R. sect. *Anarrhichomenum* p. 755
    oo. Plants not as above.
      p. Erect herbs, shrubs or trees, inflorescence compact, if an open panicle or raceme then with a conspicuous cicatrix.
        q. Flowers solitary or not more than 3 at a node, peduncle not evident ---- G. sect. *Pseudo-capsica* p. 713
        qq. Flowers in pedunculate inflorescences mostly of more than 3 (subgenus *Solanum* p. 733).
          r. Herbs; inflorescences soon lateral, the cicatrix not prominent; fruits at least partly purple black ---- N. sect. *Solanum* p. 733
          rr. Shrubs or trees; inflorescences opposite the leaves, the cicatrix conspicuous; fruits variously colored ---- O. sect. *Leiodendra* p. 739
      pp. Scandent shrubs or herbs, sometimes lianas; inflorescences open; cicatrix mostly not conspicuous (subgenus *Potatoe* p. 750).
        s. Pedicels articulated near the middle; tuber bearing; aromatic herbs ---- P. sect. *Petota* p. 750
        ss. Pedicels articulated near the base; not tuberbearing; not aromatic.
          t. Leaves all simple and entire.
            u. Creeping plant; leaves less than 3.5 cm long; inflorescence few- to several-flowered ---- R. sect. *Anarrhichomenum* p. 755
            uu. Large woody vine; leaves more than 3.5 cm long; inflorescence many flowered ---- T. sect. un-named p. 758
          tt. At least some leaves compound or lobed.
            v. Calyx truncate or nearly so, not splitting at the sinuses.
              w. Inflorescence axes slender; anthers short and stout; corolla glabrate outside ---- S. sect. *Jasminosolanum* p. 757
              ww. Inflorescence axes stout; anthers long and slender; corolla densely puberulent outside ---- T. sect. un-named p. 758
            vv. Calyx with manifest lobes, splitting at the sinuses ---- Q. sect. *Basarthrum* p. 752

Subgenus **Leptostemonum** (Dun.) Bitt., Bot. Jahrb. Syst. 55: 69–89. 1919.

Section *Leptostemonum* Dun. *in* DC., Prodr. 13(1): 29–31, 183–371. 1852. LECTOTYPE: *S. mammosum* L.

Shrubs, *trees*, *vines* or perennial *herbs*, mostly armed, pubescence of stalked or sessile stellate hairs,[4] sometimes with bristles. *Leaves* entire or lobed, seldom toothed, glabrous to densely pubescent and often armed; minor leaves sometimes present. *Inflorescence* mostly lateral, a reduced panicle or raceme, the peduncle simple or commonly once-branched, often elongating in fruit; pedicels deciduous at the base, sometimes leaving a conspicuous cicatrix. *Flowers* small to large, sometimes zygomorphic, often displaying developmental polygamy; calyx splitting at the sinuses and becoming deeply lobed, sometimes accrescent and loosely or tightly enveloping the fruit; corolla deeply or shallowly lobed, white, blue, purplish, or yellow; stamens equal or not, the anthers mostly slender, tapering to the tip and opening by small terminal pores, or if stout then abruptly narrowed to a small tip and often opening also by longitudinal slits near the base, dehiscing introrsely or extrorsely by outward bending of the tips; ovary glabrate to tomentose. *Fruit* a dry, juicy, fleshy, mucilaginous or rarely woody berry, sometimes very large, glabrous or pubescent; seeds mostly flattened, sometimes winged, rarely prismatic.

This subgenus is for the most part well defined by its stellate pubescence, armament, and the shape of the anthers. In Panama the subgenus is represented by sections *Acanthophora*, *Melongena*, *Lasiocarpa*, *Micracantha*, and *Eriophylla*. Species are often developmentally polygamous, *i.e.* The first flowers are staminate and later flowers are perfect.

A. Section **Aculeigerum** Seithe, Bot. Jahrb. Syst. 81: 291–292. 1962. TYPE: *S. wendlandii* Hook. f.

Mostly armed, glabrous *shrubs*, scandent *herbs* or high-climbing *lianas*; stems green, glabrous with stout, orange, recurved spines. *Leaves* mostly pinnately compound or deeply lobed, variable in shape on the same plant, sometimes entire, mostly armed with stout recurved spines on the main veins beneath, sometimes with erect pauciradiate hairs on the lamina; petioles mostly armed, minor leaves wanting. *Inflorescence* a large, terminal or lateral, many-flowered panicle, ebracteate, pedicel scars evident but not raised, well spaced. *Flowers* mostly large, showy; calyx campanulate, splitting deeply at the sinuses; corolla rotate, shallowly lobed; stamens unequal, one longer than the others, connivent, elongate but hardly tapering, opening by small terminal pores; ovary glabrous.

Plants in this section display an unusual combination of characters and the section has been subject to varying placement by different workers. Leaves and inflorescences bear similarity to those of some species here placed in subgenus *Potatoe*. The spines, however, are like those of *S. jamaicense*, *S. lancaeifolium*, *S. torvarum*, or many other species of subgenus *Leptostemonum*. The anthers of this section are long and slender with small terminal pores which might be

interpreted as indicative of either subgenus *Leptostemonum* or *Potatoe*. This group may warrant distinct subgeneric status.

This section includes several species of the New World ranging from Mexico to Argentina.

1. **Solanum wendlandii** Hook. f., Bot. Mag. *Tab. 6914*. 1887. TYPE: Cultivated from Costa Rican seed, collector not indicated (K).

Prostrate or scandent *vine*, sometimes high climbing in the canopy; stems green, glabrous, herbaceous with occasional recurved spines. *Leaves* to 20 cm long and 15 cm broad, entire or deeply 3–7-lobed, usually both on the same plant, the lobes ovate, acuminate apically, the sinuses broadly rounded, bearing large recurved spines on the midrib and petiole; petiole 3–5 cm long. *Inflorescence* showy, many-flowered; calyx 5 mm long, lobed to ½–⅓ the way down; corolla blue-purple, large, 5 cm across, rotate, the lobes very shallow; stamens linear, unequal but appearing equal as the one long anther is bent to meet the tips of the other 4, these 8 mm long, with yellow or purplish tips; ovary glabrous. *Fruit* not seen.

This species is readily identifiable by its lobed leaves and unexpected but inescapable spines. The large panicles of colorful flowers make it an excellent garden subject. This species is a widely cultivated ornamental in tropical gardens.

CHIRIQUÍ: Palo Santo, 3 mi. N of Volcán, *Croat 13547* (DUKE, F, MO, SCZ). S side of Cerro Pando, 6,000 ft, no evidence of habitation here, *D'Arcy 5410* (MO, PMA). Cultivated, town of Boquete, on fencerow, *D'Arcy 5449* (MO). From Boquete to 3 mi. N, 3,300–4,200 ft, second growth, cultivated areas and roadsides, *Lewis et al. 362* (MO). COCLÉ: N rim (wet) of El Valle, *Allen 1823* (MO). Upland woods 5–9 mi. NW of El Hato de Volcán on road towards Costa Rica, 5,500 ft, *Luteyn 852* (MO).

B. Section **Eriophylla** Dun., Hist. Sol. 127. 1813. LECTOTYPE: *S. jamaicense* Mill.

Shrubs somewhat scandent, mostly armed with recurved spines, pubescent with porrect or multangulate stellae. *Leaves* mostly sinuate-lobed, basally cuneate and sessile, often spiney. *Inflorescence* lateral, a short raceme on the stem; peduncle unbranched. *Flowers* with the calyx splitting at the sutures as the fruit and flower egress; mostly provided with bristles and sometimes with spines; corolla deeply lobed; stamens equal; style sometimes pubescent. *Fruit* a globose, juicy, glabrous berry; seeds compressed.

This section may be monotypic. It is distributed from Mexico to well into South America and is present in Florida and the Antilles.

2. **Solanum jamaicense** Mill., Gard. Dict., ed. 8. 1768. TYPE: Jamaica, *Houston*, Herb. Sloane 107 (BM).

S. brevipilum Dun., Hist. Sol. 191, *tab. 21*. 1813. TYPE: ?St. Thomas, *Riedlé s.n.* (MPU, P).
S. cuneifolium Dun., Hist. Sol. 193, *tab. 22*. 1813. TYPE: (not seen).
S. heterotrichum Dun., Hist. Sol. 192, *tab. 20*. 1813. TYPE: Fragment "*Dun. 1813*" (MPU).
S. brevipilosum Dun. *in* DC., Prodr. 13(1): 199. 1852. LECTOTYPE: Brazil, *Salzman 384* (G-DC).

S. portoricense Dun. *in* DC., Prodr. 13(1): 374. 1852. TYPE: Portorico, *Riedlé s.n.* (B-W, not seen; IDC 7440. 301: II. 4).

Erect or straggling *shrub* to 3 m tall; stems very densely tomentose, the pubescence with an ochraceous cast, of variously stalked, often dendritic, subechinoid stellae with long and torulose radii, and also of scattered hairs bearing one very long arm, armed with short (5 mm long), stout-based recurved spines. *Leaves* thick, 4–15 cm long, ovate, rhombic or obovate, often almost as broad as long, typically acute apically, basally long-acuminate, encompassing the petiole almost to the base, the leaves thus subsessile, the margins entire or usually shallowly angular-sinuate, both surfaces with dispersed, stalked pauciradiate non-porrect stellae. *Inflorescence* lateral, a short raceme, sometimes subumbellate; peduncle short with long-stalked and hydroid bristles, some of these dendritic; pedicels 2 cm long, slender, villous. *Flowers* very small; calyx 4 mm long, lobed about ½ the way down, the lobes narrowly lanceolate to subulate and bearing prominent dendritic-hydroid bristles; corolla white, 8–11 mm across, lobed ½ the way down; stamens equal, the filaments very short (0.2 mm long), glabrous, the anthers 3–4 mm long, elongate-attenuate, opening by relatively large terminal pores and sometimes ultimately by longitudinal slits; style sometimes pubescent. *Fruit* a juicy, red, shiny berry 5 mm across; seeds 1.5–2 mm across, lenticular, orange, foveate.

This species is a salient feature of roadside vegetation in lowland central Panama, the straggling, brownish felty shrubs forming thickets or standing alone in areas of recurring disturbance. The inconspicuous flowers, red fruits, and triangular leaf bases are also distinctive. *Solanum jamaicense* is widespread, occurring in Florida, Mexico, the Antilles, Central America, and parts of South America.

CANAL ZONE: Without locality, *Blum 678* (MO, PMA). Near TTC Albrook Tower, *Blum 1084* (MO). Lighthouse clearing, Barro Colorado Island, *Croat 11618, 11987* (both MO). Near Hill C-6, Ft. Sherman, *Duke 4357* (MO), *4399* (GH, MO, US). Ancón Hill, *Duke 4578* (GH, MO). Albrook, U. S. Army Tropic Test Center, *Dwyer 7121* (GH, MO). Gamboa Naval Reservation, second growth forest, *Ebinger 897* (GH, MO, US). Ancón Hill, *Killip 3030* (MO). Miraflores Locks area, *Tyson 1143* (MO). Old Fort San Lorenzo, *Tyson 1548* (MO). Fort Sherman on Peña Road, *Tyson & Ah Chu 1687* (MO). One mi. N of Summit Garden, *Tyson & Blum 1976* (MO). COLÓN: Near Río Piedras along road to Portobelo, *Blum et al. 2495* (MO). Road to Portobelo ¼ mi. N of Maria Chiquita, *Croat 11356* (MO). DARIÉN: Río Balsa between Manene and Areti, *Duke 13508* (MO, US, WIS). Near Pucro, Río Paya, *Stern et al. 219* (GH, MO, US). HERRERA: Between Las Minas & Pesé, *Duke 12316* (MO). PANAMÁ: Near Cerro Azul 3 mi. above Goofy Lake, *Croat 11585* (MO). Near top of Cerro Campana along highway, *Croat 12079* (MO). Halfway between El Llano and Río Mamoni along Pan American Highway, *Duke 5537* (MO). Tocumen, *Dwyer & Hayden 18* (MO). Cerro Azul, *Dwyer 1525* (F, MO). Goofy Lake toward Cerro Azul, ca. 2 mi. S of Goofy Lake, *Dwyer & Stimson 8070, 8075* (both MO). La Campana, Cerro Campana, wooded area along road, *Ebinger 332* (MO, US). Cerro Azul, selva alta perennifolia, 20 km desviación, *Gomez-Pompa et al. 3422* (MO). Cerro Jefe down slope from summit, *Kirkbride & Crebbs 14* (MO, NY, PMA). Cerro Campana, cloud forest, *Lewis et al. 3087* (DUKE, MO, UC). Río Chagres tributary 5 mi. SW of Cerro Brewster, 1,000 ft, *Lewis et al. 3438* (MO). Cerro Jefe, *Tyson et al. 4307* (MO). Cerro Campana, 2,500 ft, *Tyson 6441* (SCZ). Cerro Azul, *Wendehake 1* (MO, PMA). Near Arraijan, thickets and forests, ca. 15 m, *Woodson et al. 1391* (A, F, MO, NA, NY). SAN BLAS: Mulatuppu (Río Ibedi), "mogosan," used by Cuna for stomach ache, *Duke 8467* (MO, US). Headwaters of Río Multappu, seasonal evergreen forest, *Elias 1731* (MO). VERAGUAS: Between Tolé and Santiago, 50 mi. W of Santiago, *Kirkbride & Hayden 165* (MO, NY).

C. Section **Micracantha** Dun., Hist. Sol. 128, 193. 1813. TYPE: S. *micracanthos* Lam.

Vines, sometimes high climbing, sometimes shrub-like, mostly copiously armed with recurved spines, pubescent with porrect and multangulate stellate, sometimes with stout bristles. *Leaves* sinuate lobed to entire, variable on the same plant, often spiny. *Inflorescence* lateral, a short raceme or subumbellate-fascicled on the stem, the peduncle unbranched. *Flowers* narrowly cylindrical or tapering in bud, the calyx splitting at the sutures as the flower and fruit egress; mostly with bristles and sometimes spines; corolla deeply divided into narrow lobes; stamens equal, connivent into a tube; ovary sometimes pubescent. *Fruit* a globose, juicy glabrous or pubescent berry; seeds compressed.

Species in this section may be recognized by the narrow and elongate flowers and by the usually copiously armed stems and leaves. Only S. *jamaicense* in Panama (sect. *Eriophylla*) has similar scandent, pubescence, and armament features; it may be distinguished by its tiny flowers and cuneate leaves. Plants in this section are widespread weeds, known under many different names but probably consisting of only a few species.

a. Seeds less than 2.5 mm across; fruit mostly less than 1 cm across; corolla glabrous within; plants only occasionally copiously bristly ..... 3. S. *lancaeifolium*
aa. Seeds more than 3.5 mm across; fruit more than 2 cm across; corolla somewhat pubescent within; plants mostly copiously bristly ..... 4. S. *siparunoides*

3. **Solanum lancaeifolium** Jacq., Coll. 2: 286. 1788; Ic. Pl. Rar. 2: 11, *tab.* 329. 1787. LECTOTYPE: *Jacquin, s.n.* (W; BM, isolectotype).—FIG. 19.

S. *flexuosum* Vahl, Eclog. Amer. 1: 22. 1796. TYPE: ?Trinidad, *Rohr s.n.* (BM).
S. *scabrum* Vahl, Eclog. Amer. 1: 22. 1796. TYPE: ?Trinidad, *Rohr 94* (C).
S. *sarmentosum* Lam., Illustr. 2: 24. 1794. TYPE: St. John (?Tortola), *Richard s.n.* (P).
S. *enoplocalyx* var. *mexicanum* Dun. *in* DC., Prod. 13(1): 223. 1852. TYPE: Mexico, *Berlandier 48* (G-DC, P).
S. *lancaeifolium* var. *punctato-maculatum* Dun. *in* DC., Prod. 13(1): 222. 1852. TYPE: Trinidad, *Sieber 132* (G-DC, MO).
S. *donnell-smithii* Coult., Bot. Gaz. (Crawfordsville) 16: 144. 1891. TYPE: Guatemala, *Donnell Smith 2268* (NY, US).
S. *abbottii* Leonard, Jour. Washington Acad. Sci. 14: 415. 1924. TYPE: R. Dominicana, *Abbott 2073* (US).

Vine, 1–100 m long, sometimes shrub-like; stems glabrate to stellate-tomentose, often with stout bristles, armed with short, recurved spines. *Leaves* 3–25 cm long and 2–10 cm broad, lanceolate to elliptic, entire or usually with sinuate-dentate margins, glabrate to tomentose or hispid with mostly sessile stellae, armed on the midrib or minor veins; petioles mostly armed, less than ⅓ the length of the leaf. *Inflorescence* lateral, few-to several-flowered; peduncle short, mostly unbranched, 5–15 mm long, filiform, becoming longer and stouter in fruit. *Flowers* mostly small; calyx 1–2 mm long with the lobes ca. 1 mm long, splitting at the sutures and enlarging in fruit, often armed with straight spines; corolla (Panama) mauve to purple outside, white inside, divided almost to the base, pubescent outside, the lobes often recurving 7–12 mm long; anthers slender and tapering to the tips, converging to form a tube or free, about as long as the corolla lobes.

FIGURE 19. *Solanum lancaeifolium* Jacq.—A. Branch with flowers (× ¾). [After *Dodge et al. 16652* (MO).]—B. Branch in fruit (× ¾). [After *Correa 84* (MO).]

Fruit a shiny, red or orange, globose, juicy berry, 8–15 mm across; seeds yellowish, flattened, 2.5 mm across.

This species, known in Panama as "araña gato," is one of the most noxious and ubiquitous weeds of roadsides, pastures, and cultivated lands. It ranges from Mexico to Brazil and is present in the West Indies. Mainly a lowland species, it does ascend to middle elevations.

This species is very plastic, its leaves, pubescence and inflorescence vary from district to district, from plant to plant, and from one part of a single plant to another. Measurements of stomata size strongly suggest presence of polyploidy at several levels, although the only published chromosome count is that of a diploid, $n = 12$. Plants of the Antilles are generally less pubescent, the flower color is white and the berries are scarlet; only occasional Panamanian plants show this combination of characters. An examination of specimens from a wide geographical range argues for taxonomic recognition of only a single polymorphic species.

BOCAS DEL TORO: Near Almirante, marshy area, *Croat 16504* (MO). Changuinola, *Dwyer 4630* (MO). Río Changuinola, *Dwyer 6422* (MO). Chiriquicito to 5 mi. S along Río Guarumo, rain forest by river, *Lewis et al. 1989* (GH, MO, US). Isla Colón, *Wedel 493* (GH, MO). Water Valley, *Wedel 938* (MO). Near Chiriquí Lagoon, *Wedel 1335* (GH, MO, US). CANAL ZONE: Near Summit Garden, *Croat 12539* (MO). Near Summit Naval Radio Station, *Croat 12855* (MO). Between Madden Wye and Summit Naval Radio Station along old road, *Croat 15021* (ADW, MO). Cocoli, shade in parking area by stream, *D'Arcy 3941* (MO). Chagres, *Fendler 253* (G, GH, MO, US). Fort Clayton, *Greenman & Greenman 5172* (MO). Las Cruces Trail, government forest, 75 m, *Hunter & Allen 749* (MO). Madden Forest Preserve along Las Cruces Trail and highway, deep rain forest, *Lewis et al. 5344* (MO). Between railroad and Panama Canal, 3 mi. W [?] of Gamboa, *Nee & Mori 3598* (MO). Old Fort San Lorenzo, *Tyson 1555* (MO). Fort Clayton near old hospital building, *Tyson & Blum 3927* (MO). Río Providencia 12 mi. S of Colón, *Tyson & Blum 3935* (MO). Barro Colorado Island, *Croat 5252, 7217, 7441, 8327, 8915* (all MO), *9027* (DUKE, MO), *13209* (MO), *14914* (BIRM, C, MO, MPU); *D'Arcy 3923, 4297* (both MO); *Dwyer 1413* (MO); *Ebinger 137* (MO); *Shattuck 46, 180* (both A, MO), *477* (MO, US); *Wetmore & Abbe 39* (A, GH, MO). CHIRIQUÍ: Between David and Concepción, *D'Arcy 4229, 4230* (both MO). Between El Hato de Volcán and Concepción, grown-up weedy pasture, *D'Arcy 4258* (MO). Western Chiriquí lowland, *D'Arcy 4266, 4278* (MO). Puerto Armuelles, *D'Arcy 4279, 4281* (both MO). Progreso, *D'Arcy 4285, 4286* (both MO). Near Río San Juan, pasture weed, *D'Arcy 4291* (MO). West of Concepción, Pan American Highway 7 mi. E of Río Gariche, *D'Arcy 5424* (MO). Above Paseo la Canoa, 2,100 ft, *D'Arcy 5434* (MO). Just outside of Gualaca, *D'Arcy 5482* (MO). Boquete, Cerro Horqueta 5,000–6,000 ft, dense woodland in cloud forest, *Dwyer & Hayden 7760* (MO). Boquete 6 mi. N of Concepción, second growth forest, *Ebinger 755* (MO). COCLÉ: 20 mi. S of Nata, *D'Arcy & Croat 4118* (MO). Cerro Pilón, 2,700 ft, *Lallathin 8084* (MO). Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte, advanced secondary rain forest, *Lewis et al. 5573* (MO, W, WIS). Between Las Margaritas and El Valle, *Woodson et al. 1770* (A, MO, NA, NY). COLÓN: Río Chagres, Juan Mina plantation, region above Gamboa, *Allen 4127* (MO). Río Miguel de la Borda near Guasimo, forested area, *Croat 9907* (MO). SW of Portobelo 4 mi. along river, *Croat 14120a* (MO). Garotte, ca. 10 mi. NE of Portobelo on coast, weed patch behind village, *D'Arcy 3997* (MO). Portobelo, weed along fenceline, *D'Arcy 4058* (MO). Just W of Portobelo, wet ravine, *D'Arcy 4080* (MO). DARIÉN: Wooded ridge just S of El Real, *Duke 5056* (MO). Río Sambu 0–5 mi. above Río Venado, *Duke 9271* (US), *9272* (MO, US). Agua Fría ca. 8 mi. N of Santa Fé, *Duke 10112* (MO, US). Near Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 866* (MO). HERRERA: Near Ocú, *Allen 4079* (MO). Just S of Ocú, *D'Arcy 4132* (MO). LOS SANTOS: 3 mi. S of Carreta, ca. 5 mi. S of Las Tablas, *Burch et al. 1247* (MO). Side of main highway 10 km S of Chitré, *Correa 84* (DUKE, MO, PMA). Fencerow, 7 mi. S of Chitré, *D'Arcy & Croat 4168* (MO). Weedy pasture 7 mi. S of Chitré, *D'Arcy & Croat 4179* (MO). Shrubby

pasture 6 mi. S of Las Tablas, *D'Arcy & Croat 4182* (MO). Between Limon and Punta Mala, *D'Arcy & Croat 4212, 4213* (both MO). Punta Mala, headland in full wind and salt spray, *D'Arcy & Croat 4214* (MO). Río Tonosí near Tonosí, *Lewis et al. 1546, 1547* (both MO). Río Pedregal headwaters, 25 mi. SW of Tonosí, *Lewis et al. 2926* (F, MO, PMA). 12 mi. S of Macaracas, *Tyson et al. 3070* (MO). PANAMÁ: Side road off Inter-American Highway 1 mi. E of Tocumen airport, *Blum & Tyson 1952* (MO). Bank of Río Sajalices S of Capira, *D'Arcy 5261* (MO). Between Panamá and Chepo, *Dodge et al. 16652* (G, MO). Inter-American Highway just E of Bejuco, *Duke 4554* (MO). Panamá Viejo, *Duke 5716* (GH, MO). Tocumen, *Dwyer 4561, 4591, 5131* (all MO). Near Las Sabanas, *Killip 3090* (MO). Near Tapia River and Juan Díaz, *Killip 3093* (MO, US). Peaks of Cerro Trinidad, saddle on SE slope, degraded cloud forest, *Kirkbride & Duke 1661* (MO). Savanas, *MacBride 2669* (G, US). Road to Panama City W of Chepo, *Tyson 5368* (FSU, MO). Río Tatare, *Woodson & Schery 1006* (MO, US). VERAGUAS: Headwaters of Río Cañazas, trail between Cañazas and foot of Cordillera Central, 300–600 m, *Allen 156* (MO). Old Interamerican highway 1 mi. W of Santiago, *Tyson 5160* (MO). PROVINCE UNKNOWN: North coast of Colombia, Panamá, year 1832, *Cumming 1134* (BM).

4. **Solanum siparunoides** Ewan, Chicago Acad. Sci. Nat. Hist. Misc. 94: 1. 1952. TYPE: Colombia, *Smith 100* (F).

Vine, *shrub* or ?*tree* to 7.5 m high; twigs mostly densely clothed with stiff, bristles 2–6 mm long and short-stalked, porrect, pauciradiate stellae, armed with short (2 mm long), stout-based, compressed, recurved spines. *Leaves* 7–11 cm long and 2.5–4 cm wide, lanceolate or obovate, acute, acuminate or rounded apically, basally acute, obtuse or rounded, often oblique, margins entire or slightly undulate, vestite with sessile, porrect, pauciradiate hairs, those on the upperside with very long (1–2 mm) midpoints and the radii mostly reduced and fused with the leaf lamina, those beneath mostly without midpoints, armed on both sides with short spines and copiously armed on the midvein beneath; petiole 0.5–3 cm long, bearing stellae, bristles and recurved spines. *Inflorescence* a simple lateral raceme; peduncle 4–5 cm long, becoming stout in fruit, with stellate hairs and conspicuous bristles; pedicels drying dark, slender, 6–10 mm long, elongating to 15 mm long and becoming very stout in fruit, bearing straight spines. *Flowers* relatively large; calyx 4 mm long, the lobes densely vestite with straight, flattened spines 2–3 mm long, in fruit becoming 20–22 mm long, deltoid, stout and woody; corolla lobed almost to the base, the lobes narrowly lanceolate, 2.5 cm long, pubescent inside with tiny sessile echinoid hairs, outside with stellae having long midpoints and also long radii, filaments glabrous, the anthers lanceolate, 10 mm long. *Fruit* red, large (3.5 cm across), glabrous; seeds lenticular-discoid, 4–5 mm across.

This species is much like *S. lancaeifolium* but has much larger fruit and seeds and the corolla is pubescent within. In overall appearance it is usually even more formidable than *S. lancaeifolium*. One collection, *Busey 914*, lacks bristles and the leaves are merely scarbidulous, not hispid. The fruits and seeds are of the dimensions of other collections cited. Several collections of *S. lancaeifolium* from Central America match this species in general but lack the large fruits and seeds and the pubescent corolla.

CANAL ZONE: Pipeline road, premontane wet forest area, *Gentry 1945* (MO). PANAMÁ: 10 km N of El Llano on road to Cartí, 400 m, *Busey 914* (MO). Near Altos de Pacora (10 mi. beyond Goofy Lake), *Croat 14416* (F, DUKE, MO, SCZ). Cloud forest on Cerro Campana

above Su Lin Motel, *Croat 14732* (MO). 1 mi. N of Cerro Azul, 2,300 ft, *Tyson & Blum 4078* (MO).

D. Section **Lasiocarpa** (Dun.) D'Arcy, Ann. Missouri Bot. Gard. 59: 270. 1972. [1973].

Subseries *Lasiocarpa* Dun. *in* DC. Prodr. 13(1): 30, 252–258. 1852. LECTOTYPE: *S. lasiocarpum* Dun.

Large *herbs, shrubs* or small *trees*, pubescent with stellate, glandular or rarely apparently simple hairs, often armed with acicular spines. *Leaves* membranaceous to felty, often villous or tomentose and armed, mostly repand, lobed or dentate. *Inflorescence* a several-flowered, lateral, congested, mostly unbranched raceme. *Flowers* with the calyx deeply lobed, mostly somewhat accrescent in fruit, sometimes subfoliaceous; corolla deeply lobed; stamens equal, very variable as to filament length and anther shape, but the anthers in most species with a contracted apex and minute pores; ovary pubescent with stellate hairs. *Fruit* manifestly pubescent at least until nearing maturity; seeds flattened.

This section is seemingly related, because of its large fruits, broadly ovate leaves, and sometimes simple hairs, to section *Acanthophora*. *Solanum pectinatum* is in some respects intermediate between the two sections, having mostly derived simple hairs on the stems and sometimes on the leaves, and the mature fruit is glabrous. However, the presence of a dense tomentum of stellate hairs on the young fruit places it in sect. *Lasiocarpa*. The broad, almost deltoid calyx lobes are another significant feature frequent in sect. *Lasiocarpa*. Some species are also suggestive of section *Melongena*. The species considered here, however, are closly related and do not conform satisfactorily to either of the above sections. They are readily recognized by their pubescent fruit and accrescent calyx. The section is best represented in tropical America, although S. *flavescens* ranges into temperate Mexico, and S. *ferox* L., of southern Asia, is a member of this section.

a. Hairs of leaves and stems mostly appearing simple; mature fruits glabrous, shiny ..... 9. S. *pectinatum*

aa. Hairs of leaves and stems stellate; mature fruits pubescent, dull.
  b. Tomentum white but suffused with purple.
    c. Leaves large, many exceeding 25 cm long; fruits large, more than 4 cm across, the tomentum easily rubbed off when mature ..... 10. S. *quitoënse*
    cc. Leaves smaller, less than 20 cm long; fruits smaller, less than 3 cm across, the tomentum persistent.
      d. Stellae of the stems mostly sessile with long midpoints ..... 8. S. *hirtum*
      dd. Stellae of the stems mostly long-stalked with short midpoints ..... 7. S. *flavescens*
  bb. Tomentum whitish with a rusty or brownish cast.
    e. Fruit pilose, the stellae more than 1 mm long ..... 7. S. *flavescens*
    ee. Fruits short tomentose or hispidulous, the stellae less than 1 mm long.
      f. Flowers purple; fruits with stellate hairs ..... 6. S. *erythrotrichum*
      ff. Flowers white; fruits with mostly simple hairs ..... 5. S. *accrescens*

5. **Solanum accrescens** Standl. & Mort., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1075. 1938. TYPE: Costa Rica, *Skutch 2979* (US).

S. *erythrotrichum* sensu Standl. Contr. U. S. Natl. Herb. 27: 331–332. 1928, non Fern.

Shrub or small *tree* to 5 m tall; twigs reddish with long, multiseriate-stalked stellae which usually have long midpoints, armed with short, slightly recurved spines. *Leaves* to 25 cm long, entire, broadly ovate or elliptical, apically acuminate, basally rounded, above with dispersed to dense, sessile, multangulate hairs, the arms long and slender; beneath tomentose with smaller sessile hairs and with long-stalked hairs as well, the major veins conspicuous; petioles 3–4 cm long, usually unarmed. *Inflorescence* lateral, several-flowered, on a straight, stout, tomentose peduncle 3–4 cm long; pedicels stout, 5–10 mm long, not much enlarged in fruit. *Flowers* with the calyx 10 mm long, deeply lobed, the lobes accrescent in fruit and becoming foliaceous, broadly or narrowly ovate, tomentose outside and hirsute at the apex inside; corolla white, 3 cm across, lobed nearly to the base, the lobes lanceolate, tomentose outside, glabrous within; anthers 7–9 mm long on short filaments, broad at the base and narrowing in the upper portion; ovary densely pubescent, the style glabrate. *Fruit* globose, to 15 mm across, densely viscid-pubescent with short, glandular, simple hairs, a few scattered stellate hairs often present; seeds lenticular, pinkish, 3–4 mm long.

The fruit of this species is often persistent on the tree until the pericarp has withered away leaving the pinkish seeds exposed. At no stage is the fruit soft or juicy. *Solanum accrescens* is somewhat variable as to density of pubescence, most plants being definitely wooly on the young parts, but on a few collections the leaves are membranaceous and merely soft tomentose. Panamanian material differs from Costa Rican in pubescence, the stellae of having distinct midpoints, the result being a tomentose rather than puberlent appearance.

The species is also very like *S. rubidum* Standl. & Mort. of Costa Rica, but that species has long, simple hairs on the fruits. These hairs may be midpoints of reduced stellae but material at hand is not sufficient to establish this. This species is apparently similar to *S. brachybotryon* Dun. *in* DC., from Surinam, the type of which was not seen. The protologue of *S. brachybotryon* gives no indication of the structure of the stellate hairs.

A plant of roadsides and forest openings, *S. accrescens* is to be found in Panama at lower and middle elevations.

CANAL ZONE: Madden Forest, side of disused gravel road, *D'Arcy 5244* (MO). Cerro Pilón, *Lallathin 5032* (MO). El Valle de Antón, 1,000–2,000 ft, edge of cloud forest and roadside, *Lewis et al. 2503* (MO). Mountains above El Valle, weedy area beside dirt road, *Stimson 5025* (SCZ). PANAMÁ: E slope of Cerro Jefe, 2,700 ft, *Blum & Duke 2201* (FSU, MO, SCZ). One mi. W of Motel Su-Lin along dirt road to Cerro Campana, 2,500 ft, *Correa 367* (MO). Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 458* (MO). Cerro Azul, *Croat 13026* (SCZ). Cerro Campana, end of road beyond Su Lin Motel, *Croat 14223* (F, MO, SCZ). In cafetal, Cerro Jefe, *D'Arcy 3970* (MO). Cerro Campana, *D'Arcy & Dressler 5503* (MO). Cerro Jefe, *Duke 9383* (MO). Cerro Azul, Goofy Lake, *Dwyer 1520* (BM, MO). Goofy Lake to 8 mi. S toward Cerro Jefe, *Dwyer 7054* (GH, MO, US). 2–3 mi. S of Goofy Lake, road to Cerro Jefe, 2,000–2,200 ft, lower elevations of cloud forest, *Lewis et al. 267* (MO). Cerro Campana, cloud forest, *Lewis et al. 3032* (MO). 5 mi. SW of Cerro Brewster, tributary of Río Chagres, 1,000 ft, sandy and rocky river banks, *Lewis et al. 3470* (MO). One mi. N of Goofy Lake, edge of cultivated field, *Oliver et al. 2679* (MO). Cerro Campana above Su Lin Motel, rain forest, *Porter et al. 4163* (MO). Summit of Cerro Campana, rain forest, *Porter et al. 4896* (MO). Without locality, *Seemann 1197* (BM). E of Río Tocumen near the big swamp, wet forest, *Standley 26560* (US). Cerro Jefe in Clusia forest, 2,700–3,000 ft, *Tyson et al. 3321* (MO, SCZ). Top of Cerro Jefe, 2,700–3,000 ft, *Tyson et al. 4350* (FSU, MO, SCZ).

6. **Solanum erythrotrichum** Fern., Proc. Amer. Acad. Arts 35: 561. 1900. TYPE: Guatemala, *Türckheim 1381* (GH, K).

Shrub 1 m tall; twigs finely tomentose with appressed, ferrugineous, porrect stellae which have reduced midpoints, armed with short, stout, flattened, recurved, dark-colored spines, 2–3 mm long. *Leaves* unarmed, 12–15 cm long, broadly elliptical, irregularly sinuate-dentate, apically acuminate to obtuse, basally obtuse, sometimes dimidiate, above with dispersed, subsessile, porrect stellae, their midpoints absent or much reduced, beneath with stalked or sessile, long-armed multangulate white hairs, their midpoints nearly absent; petioles 2–3 cm long, unarmed; minor leaves sometimes present. *Inflorescence* lateral, several-flowered, congested on a finely tomentose, erect peduncle 1.5–3.5 cm long; pedicels 5 mm long, becoming stout but not longer in fruit. *Flowers* with the calyx 10 mm long, deeply lobed, the lobes sub-foliaceous, 8 mm long, lanceolate, tomentose outside and dispersed-pubescent inside with sessile, porrect, ferrugineous stellae, the midpoints much shorter than the arms; corolla deep purple to purplish white, 3 cm across, lobed nearly to the base, the lobes unequal, lanceolate, tomentose outside; anthers 6–7 mm long, tapering, opening by relatively large terminal pores; ovary tomentose, the style pubescent, more so on the lower half, exceeding the anthers by 4 mm. *Fruit* globose, 12 mm across (immature), covered with fine stellae, ?glabrescent.

Solanum erythrotrichum is distinctive in the field in its purple flowers, the only other Panamanian member of this subgenus approaching it being S. *subinerme* Jacq., which differs in its truncate calyx and which has not been found in Chiriquí Province. On the herbarium sheet it may be recognized by its subfoliaceous calyx and the stellate hairs of the fruit.

Panamanian material differs from the typical Guatemalan material in its pubescence and flowers. The Guatemalan plants have abundant, long midpoints on the stellate hairs of twigs, petioles, and pedicels which Fernald referred to as "long slender naked hairs." It has somewhat smaller flowers, and larger, stouter spines.

CHIRIQUÍ: N side of Cerro Pando, 6,300 ft, *D'Arcy 5400* (MO). La "Pandura" N of Alto Lino, 4,300 ft, *Paul 880* (US).

7. **Solanum flavescens** Dun., Sol. Syn. 42. 1816. TYPE: Trinidad, *Riedlé, s.n.* (P-Juss., not seen).

S. *huitlanum* Brandeg., Univ. California Publ. Bot. 6: 192–193. 1915. TYPE: Mexico, *Purpus 7313* [*7813*] (MO).
S. *molestum* Brandeg., Univ. Calif. Publ. Bot. 7: 331. 1920. TYPE: Mexico, *Purpus 8526* (MO).
S. *boquetense* Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 22: 103. 1940. TYPE: Panama, *Davidson 817* (F, GH, MO, US).

Herb or small *shrub* to 1 m tall; twigs densely tomentose with long-stalked, multangulate hairs, sometimes becoming brownish or even golden-yellow, armed with short or long acicular spines. *Leaves* to 30 cm long, broadly ovate, sinuate-lobed, apically obtuse, basally obtuse or subcordate, often dimidiate, above densely fine tomentose with sessile stellae, the midpoints long and superficially

resembling simple hairs, the radii short, porrect, inconspicuous against the leaf surface; beneath densely tomentose with long stalked, multangulate hairs, the tips of the lobes often glabrous above or beneath, mucronulate, the principal veins sometimes armed; petioles stout, to 7 cm long, mostly armed. *Inflorescence* lateral, fascicled or subumbellate on a short, stout, tomentose peduncle to 10 mm long; pedicels 4–6 mm long, congested, becoming stout in fruit. *Flowers* with the calyx deeply lobed, the lobes obtuse, densely tomentose, the midvein apparent in the apical portion and the apical portion glabrate, somewhat accrescent and recurving in fruit; corolla white, deeply lobed, 2.5–3 cm across, tomentose outside; anthers subsessile, 12–15 mm long, stout below and coming to a fine point, the point sometimes bent outwards. *Fruit* a persistently tomentose yellow berry to 2 cm across, subtended by the somewhat accrescent calyx.

This species closely resembles *S. hirtum* from which it differs mainly in the type of pubescence, that of *S. hirtum* being of mostly sessile stellae and that of *S. flavescens* mostly of long stalked stellae. There is usually a distinct difference in the color of the pubescence as well.

This species ranges from Mexico into South America but is most common in Mexico and Guatemala. It is known in Panama from only one collection in the Chiriquí Mountains.

CHIRIQUÍ: Boquete, 3,800 ft, *Davidson 817* (F, GH, MO, US).

8. **Solanum hirtum** Vahl, Symb. Bot. 2: 40–41. 1792 [1791]. TYPE: Trinidad, *Rohr 59* (C).—FIG. 20.

Shrub or small *tree* to 5 m tall; twigs viscid-tomentose with nearly sessile, multangulate hairs, often suffused with purple, the midpoints long and gland-tipped, armed with short, sericeous, acicular spines to 7 mm long. *Leaves* to 25 cm long, broadly ovate, angular- or sinuate-lobed, apically obtuse, basally hastate, sometimes dimidiate, both sides tomentose with hairs like those of the twigs, the underside drying reticulate veined, a denser tomentum outlining the veins, the major veins often armed; petioles to 12 cm long, sparingly armed. *Inflorescence* lateral, fascicled or subumbellate on a very short to 10 mm long, stout, tomentose peduncle; pedicels 4–6 mm long, congested, becoming stout and 7–25 mm long in fruit. *Flowers* with the calyx lobed nearly to the base, the lobes elliptical or ovate with the midvein strongly marked, sometimes quite unequal, villous inside and out, 7–10 mm long in flower, becoming broader and reflexed, sometimes sub-foliaceous in fruit; corolla white, deeply lobed, 2.5–3 cm across, tomentose outside, glabrous within; anthers sessile, 12–15 mm long, stout below and abruptly narrowed to a point, bent outward at the tip so that dehiscence is extrorse; style glabrous, slightly exceeding the anthers. *Fruit* a persistently tomentose yellow berry, variable in size but sometimes attaining 2 cm across; seeds yellow, 3 mm long, compressed-lenticular.

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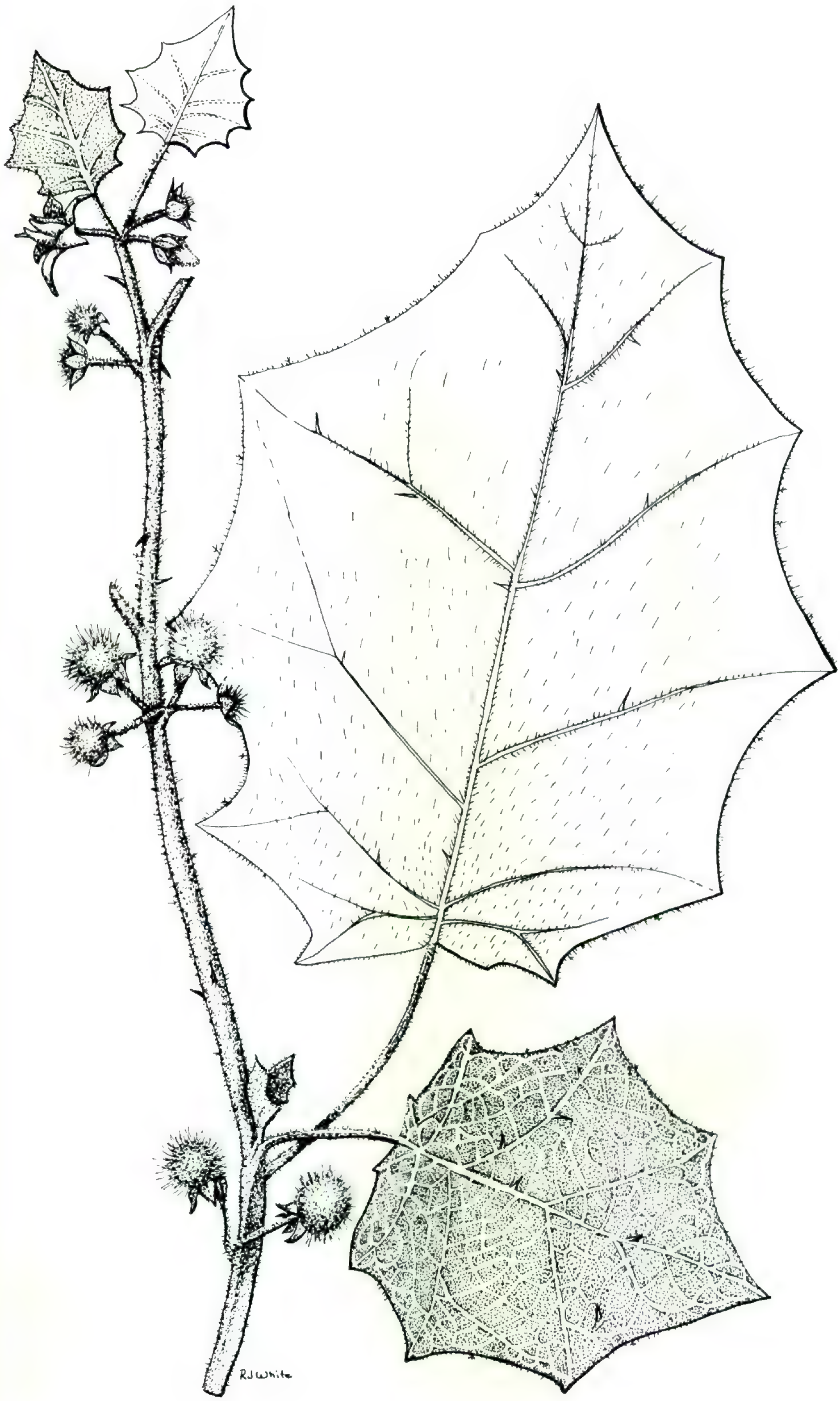
FIGURE 20. *Solanum hirtum* Vahl., branch with flowers and fruit (× ⅔). [After *Porter et al. 5164* (MO).]


R.J.White

Solanum hirtum is distinct from other Panamanian species in its consistent leaf shape, general spininess, and in the shape of the anthers. The fruits are the most densely pubescent of any Panamanian species in this section.

The species ranges from Trinidad and Colombia to the Yucatan, but most material north of Panama is at least varietally distinct, differing in having pubescent spines, stalked, multiradiate hairs on the stem, and tomentose rather than villous sepals. East of Panama, *S. hirtum* is sometimes confused with *S. stramoniifolium* Jacq., which has longer thorns, larger leaves, and an almost truncate calyx.

Most Panamanian collections are from disturbed areas in Darién.

CANAL ZONE: Cliffside, Margarita Military Base by main road, *D'Arcy 5164* (ADW, BIRM, C, F, MO, MPU, PMA, UCWI). DARIÉN: Near Pinogana, 20 m, *Allen 925* (GH, MO, NY, US). Weed near airport, El Real, *D'Arcy 5516* (C, L, MEXU, MO, WIS). Near junction of Río Peresenico and Río Pirre, *D'Arcy 5522* (MO). Road from El Real to Pinogana, *Duke 4891* (GH, MO). Pan American Highway near Boca de Cupe, *Duke 5384* (GH, MO). Cerro Piriaque, *Duke 8125* (MO). Near Yaviza, along Río Chucunaque, in cut over area by Inter American Highway, 1 km from Tuira, *Stern et al. 139* (GH, MO, US). Cerro Piriaque, 200 ft, *Tyson et al. 3842* (MO, SCZ).

9. **Solanum pectinatum** Dun. *in* DC. Prod. 13(1): 250. 1852. TYPE: ?Peru, *Poeppig 2224* (G-DC).

S. *hirsutissimum* Standl., Jour. Washington Acad. Sci. 17: 15–16. 1927. TYPE: Panama, *Pittier 5217* (US).

Herb or *shrub* to 1.5 m tall; twigs hirsute with simple hairs 3–6 mm long, these occasionally branched or stellate basally, armed with stout, orange, flattened, straight or curved spines. *Leaves* large, to 25 cm long, broadly squarrose-ovate, sinuate lobed, the base truncate or hastate, often dimidiate, the lobes often mucronate, above hirsute with mostly long, simple hairs, but often with very similar, sessile, multangulate hairs with long midpoints, beneath with similar but shorter hairs, not reticulate veined, armed above and beneath with flattened acicular spines; petioles to 10 cm long, hirsute and armed. *Inflorescence* a few-flowered lateral fascicle; pedicels 2–3 cm long, hirsute, unarmed. *Flowers* with the calyx lobed nearly to the base, the lobes large, 1–2 cm long, nearly equalling the corolla, deltoid, sometimes acuminate, hirsute outside, glabrous within except the top ⅓; corolla white, deeply lobed, hirsute outside, glabrous within; anthers 10 mm long, elongate, stout at the base and narrowing abruptly in the upper half; ovary densely tomentose, the style glabrous. *Fruit* a large, globose, shiny, orange berry to 4 cm across, losing most of its indumentum when about ½ full-size; seeds compressed-lenticular, 2 mm across.

This species is distinguished by its large shiny fruit and tomentose ovary, the overall spininess, and by the dense covering of apparently simple hairs. Some collections suggest an intermediacy between *S. hirtum* and section *Acanthophora*: *Dwyer et al. 4570* and *Porter et al. 4638* both have leaves like those of *S. hirtum*, but leaves of plants grown from their seed were typical of *S. pectinatum*. The apparently simple hairs and appearance of the mature fruits is quite like that of some species of section *Acanthophora*.

Solanum pectinatum occurs in Panama, Costa Rica, Colombia, and also Peru. It is found at the edge of forests and in abandoned cultivation at lower elevations.

CHIRIQUÍ: Along Río Dupí near sea level, *Pittier 5217* (US). COCLÉ: Cerro Pilón above El Valle, *Croat 14329* (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12200* (MO, WIS). Cerro Pilón, hill below summit above El Valle de Antón, 2,000–2,700 ft, rain forest, *Dwyer et al. 4570* (MO). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, rain forest, *Porter et al. 4638* (MO). LOS SANTOS: Los Toretos, *Dwyer 2444* (US). 11 mi. N of Tonosí, *Tyson et al. 2958* (MO, PMA), *2979* (MO, MPU). PANAMÁ: 2 mi. W of Juan Diaz, on savanas, *Killip 3101* (MO). Without locality, *Seeman 1196* (BM). Río Tatare, *Woodson & Schery 1016* (MO, US). Arraijan, *Zetek* 5568 (MO).

10. **Solanum quitoënse** Lam., Illustr. 2: 16, no. 2326. 1793 [1794]. TYPE: Herb. *Lamarck s.n.* (P).

Large *herb* or small *shrub* to 3 m tall; twigs stout, tomentose with long-armed, multangulate hairs on long, multiseriate stalks and armed with short or long, stout, flattened, yellowish spines. *Leaves* large, often exceeding 30 cm long, broadly ovate, shallowly sinuate-lobed, the lobes acuminate, the tips often glabrous above and mucronate, above with a mixture of sessile, porrect, pauci-radiate hairs with long midpoints and long, multiseriate, stalked, multangulate hairs, these latter often deciduous, beneath more densely clothed with mostly stalked stellae and suffused with purple, at least when young, armed or not on the major veins; petioles to 15 cm long, stout, tomentose and often armed. *Inflorescence* a congested fascicle or sub-umbellate raceme on a short, stout peduncle; pedicels to 10 mm long, the tomentum in part infused with purple. *Calyx* 10 cm long, lobed ½ the way down, the lobes deltoid, densely purplish tomentose outside and, except for the villous tips, glabrous within; corolla white, unequally lobed almost to the base, 5 cm across, densely tomentose outside, glabrous within; anthers subsessile, very stout at the base and narrowly abruptly in the upper ⅓, the slender tips bent outwards to allow the terminal pores to dehisce extrorsely; ovary densely tomentose, style glabrous. *Fruits* large, to 6 cm across, a yellow-orange, juicy berry, glabrescent but scabridulous until maturity, the pericarp thin, 5–10 mm thick, enclosing large, many-seeded locules; seeds lenticular-discoid, scrobiculate, with narrow but distinct wings, 3–4 mm across overall.

Solanum quitoënse may be identified in the field by its large, felty, corrugated leaves and the suffusion of purple over parts where the otherwise white tomentum is most dense. The purple color is within the hairs and not the tissues of the leaf, stem, calyx, etc. On the herbarium sheet, it is distinguished from several closely related species of South America only by close attention to details of the androecium and pubescence. All Panamanian collections are quite homogeneous as to morphology except *Duke & Nickerson 14904*, which has larger leaves and looser, shaggier pubescence than the other collections. To ascertain floral details would result in mutilation of the specimen.

The typical form of this species is unarmed, and collections of such plants are indicated below by an asterisk. Plants with spines may be referred to as fo. *septentrionale* (R. E. Schultes & Cuatrec.) D'Arcy.

This species is cultivated in crop fashion in the Chiriquí mountains for the juice of its fruits, but at the present time (1972) it must be ranked as a minor or experimental crop. Most Panamanian collections are presumed to be escapes from cultivation. It may be persistent in areas of frequent disturbance. *Solanum quitoënse* is presumed to be a native of Peru, Ecuador, or Colombia and is introduced to Panama.

CHIRIQUÍ: Finca Collins, near Boquete, *Blum & Dwyer 2569** (MO). Los Naranjos, roadside in partial shade, *D'Arcy 4274** (MO). South side of Cerro Pando, 6,000 ft, plantation crop on steep hillside, *D'Arcy 5411* (MO). Boquete, 3,800 ft, *Davidson 817* (F, GH, MO, US). Collin's Finca, 6,000 ft, cultivated in a field, *Kirkbride 111** (MO). COCLÉ: Cerro Pilón, hill below summit above El Valle de Antón, 200–2,700 ft, rain forest, *Dwyer et al. 4569* (MO). DARIÉN: Río Areti, *Duke & Nickerson 14904* (MO). PANAMÁ: Cerro Jefe, one plant, weed in catefal, *D'Arcy et al. 3952** (MO). Cerro Campana, cloud forest, 2,600–2,800 ft, *Lewis et al. 1936** (GH, MO, US).

E. Section **Melongena** Dun., Hist. Sol. 130–131, 208–218. 1813. TYPE: S. *melongena* L.

Perennial *herbs*, *shrubs* or *trees*, sometimes large, often armed, the spines stout or acicular, sometimes recurved. *Leaves* simple, entire or variously lobed, sometimes armed, pubescence of mostly porrect, sessile or stalked stellae, the stalks multiseriate and the midpoints sometimes glandular, in a few cases the hairs simple or peltate and in some cases the stalks stiff and lignified to form bristles. *Inflorescence* mostly lateral, few- to many-flowered, the peduncles branched or unbranched, terminating in racemes (cincinni), or wanting and the racemes inserted almost directly on the stem. *Flowers* medium to large; the first flowers sometimes staminate; calyx with narrow lobes which become larger as the sutures dehisce, mostly not much accrescent in fruit, sometimes armed; the corollas white, blue or purplish, mostly shallow-lobed; stamens equal, filaments glabrous, short but not absent, sometimes glandular, the anthers elongate, basally stout but narrowing to a small point, opening by small apical pores and sometimes ultimately by longitudinal slits in the basal portion; ovary mostly with some simple or stellate hairs, these often glandular, the style pubescent or not, the stigma often lobed. *Fruit* a globose, mostly glabrous, juicy, mucilaginous, rarely pulpy or fleshy berry; seeds compressed-lenticular or discoid.

This section is perhaps the largest in number of species in the genus *Solanum*, with many species in the New World and in Africa. Frequent in the humid tropics, species of section *Melongena* are also adapted to xeric regions such as northwestern Mexico, North Africa and peninsular India. The stellate hairs, structure of the inflorescence, early glabrescence of the ovary and appearance of the flower are unifying characters. In arborescent species, there is a tendency for the peduncle to branch but once shortly above the base. This tendency reappears in some species of sect. *Leiodendra* and other distantly related groups within the genus.

In Panama, section *Melongena* is considered to embrace seven species which grow wild, and except for the closely related S. *hayesii* and S. *fosbergianum*, and the distinctive S. *subinerme*, they intergrade with one another and probably with species outside of Panama. The remaining four species are widespread. *Solanum*

hartwegii displays a great variation of leaf shape, often on the same tree, but is recognizable in its blue or purple flowers and whitish lanate leaf undersides. However, hairs of similar appearance and density occur on scattered plants of S. *hispidum* and occasionally on the lowland S. *ochraceo-ferrugineum*. *Solanum torvum* is very uniform in the Antilles (the type locality is Jamaica), but in Panama it seems to intergrade into S. *ochraceo-ferrugineum* in the lowland Chiriquí-Azuero Peninsula region and shows a pattern very suggestive of introgressive hybridization. These intergrades resemble S. *madrense* Fern. of western Mexico. In the Chiriquí Mountains, often plants showing all the "marker characters" of S. *torvum* (e.g. purple pedicels, glandular pedicels, glabrate calyx sinuses) are in other respects identifiable with the plants of S. *hispidum* they are growing with. In lowland Panama, almost all plants of this alliance are S. *ochraceo-ferrugineum*, although S. *torvum* is present in infrequent colonies, and there are occasional widespread plants referable to S. *hartwegii* or S. *hispidum*.

Solanum ochraceo-ferrugineum is uniform in overall appearance throughout Panama, although it displays some regional variation. In high rainfall areas of Bocas del Toro, the Portobelo district, and Darién, the indumentum of leaf uppersides is very fine, consisting of dispersed, very short-stalked stellae with small but prominent midpoints. *Dwyer 1553* and *Johnston 1009* from Coiba and San José Islands, respectively, are the only Panamanian specimens seen with spines on pedicels and calyx. These islands are both in the Pacific off the south coast of Panama, and one might impute a geographic basis to this character, although *Duke 9527* from Isla del Rey lacks spines on the inflorescence. In the lowlands of Coclé, Chiriquí, and the Azuero Peninsula, the midpoints of the stellae are longer than elsewhere, perhaps related in an introgressive sense to similarity in the S. *torvum* growing in this area. Scattered plants suggestive of S. *hartwegii* or S. *hispidum* occur in various parts of lowland Panama, but they are rare. The area in Chiriquí around Concepción between David and the Costa Rican border and along the road to the Volcán district is an exception. Almost every plant is intermediate in appearance between S. *ochraceo-ferrugineum* and S. *hispidum*, and the frequent presence of glandular pedicels and lanate leaf undersides on some plants also suggest the presence of at least partial genomes of S. *hartwegii* and S. *torvum*. Not infrequently, clumps of shrubs are to be found in which the range of variation is very great, and the concepts of F_2 segregation or hybrid swarm are called to mind. *Solanum hispidum* itself shows a wide range of variation and may in fact be a series of species rather than a single taxon. Avoiding the temptation to recognize almost every collection as a distinct species, I considered all as one species under S. *hispidum*.

Solanum hayesii is quite uniform in appearance in lowland Panama. It is similar to S. *fosbergianum* of low elevation cloud forests. These two species do not seem to form part of the four-species group discussed above.

Solanum subinerme is also quite distinct and does not intergrade with other Panamanian species. It appears to be related to sect. *Persicariae* Dun. (type species: S. *persicaeifolium* Dun.) of the Antilles.

Besides the seven species discussed above, S. *melongena* L. occurs as a cultivated plant in Panama.

a. Flowers blue or purple.
  b. Plants whitish-lanate on leaf undersides, pedicels and calyces; native upland plants ..... 12. *S. hartwegii*
  bb. Plants pubescent but not whitish lanate; native or cultivated species.
    c. Corolla lobed less than halfway; calyx lobes becoming more than 1 cm long; cultivated species ..... 15. *S. melongena*
    cc. Corolla lobed more than halfway; calyx lobes less than 1 cm long; native lowland species ..... 17. *S. subinerme*
aa. Flowers white.
  d. Pedicels and the base of the calyx with copious glandular hairs, some of these often simple; pedicels filiform, purplish; calyx sinuses glabrate; stellae of twigs with reduced midpoints ..... 18. *S. torvum*
  dd. Pedicels and the base of the calyx eglandular or nearly so, or if glandular, then midpoints of the stellae on twigs elongate; pedicels not filiform; calyx sinuses pubescent.
    e. Flowers small, the corollas less than 3 cm across; anthers less than 4 mm long, stout, not tapering evenly to a point.
      f. Stellae on leaf undersides sessile or nearly so, not dense ..... 11. *S. fosbergianum*
      ff. Stellae on leaf undersides with long stalks, dense ..... 13. *S. hayesii*
    ee. Flowers large, the corollas more than 2 cm across; anthers more than 5 mm long, slender, tapering evenly to a point.
      g. Pubescence fine and appressed, indumentum whitish or slightly yellowish, midpoints of stellae on stem much reduced; lowland plants ..... 16. *S. ochraceo-ferrugineum*
      gg. Pubescence loose or lanate, not appressed, indumentum ochraceous to orange, midpoints of stellae on stem ample; upland plants .... 14. *S. hispidum*

11. **Solanum fosbergianum** D'Arcy.[36] TYPE: Panama, *Tyson 3536* (MO-1840657, holotype; SCZ, isotype).

Shrub or *tree* to 4 m tall; trunk straight, slender, spiny; twigs glabrescent, drying black, with sessile and subsessile porrect, ferrugineous stellae, the midpoints much reduced, unarmed. *Leaves* to 25 cm long, elliptic, oblique from a recurved midrib, apically obtuse or short acuminate, basally rounded to slightly narrowed, often dimidiate, above with dispersed, sessile, porrect stellae, the midpoints reduced or absent, beneath much as above; petioles to 6 cm long with dispersed stellae. *Inflorescence* few-flowered, often once-branched, the peduncle and rachis elongating in fruit to 5–6 cm long; pedicels 7–9 mm long, glabrescent, with sessile, porrect stellae, some bearing midpoints, in fruit elongating to 2 cm. *Flowers* small; calyx 3 cm long, lobed ⅓ the way down, the lobes deltoid, glabrous within; corolla white, deeply lobed, reflexed, 10 mm across; anthers 3 mm long, elongoid, opening by relatively large terminal pores. *Fruit* 8 mm across, dull, dirty-orange.

This species is very like S. *hayesii* but differs in its relatively sparse pubescence on the leaf underside which does not include long stalked stellae, in the more deeply lobed calyx, and in the more deeply lobed corolla. It is conspicuously different in general appearance. To date it has been found only in the lowland cloud forest of Cerro Jefe, Panamá Province. The species is named for F. Raymond Fosberg, well-known student of tropical biology.

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[36] *Solanum fosbergianum* D'Arcy, sp. nov. Frutex arborve, trunco aculeato, ramunculis non aculeatis, ramunculis foliisque nigrescentibus dum siccantibus; *Solano hayesii* similis, differt foliis utrinque sparsim pubescentibus calyceque profunde lobata.

PANAMÁ: Al lado de la carretera principal a Juan Díaz cerca del río, *Castillo 33* (MO). Finca del Indio, Cerro Jefe, *D'Arcy 5224* (MO). Cerro Jefe 4½ mi. beyond Finca Indio, *D'Arcy 5224A* (MO). Finca del Indio along Río Cascadas, Cerro Jefe, *D'Arcy 5239* (MO). Cerro Jefe, *Duke 9433* (MO). E slope Cerro Jefe, 2,800–3,100 ft, *Tyson 3536* (MO, SCZ).

12. **Solanum hartwegii** Benth., Pl. Hartw. 68. 1840–41. TYPE: Mexico, *Hartweg 498* (K).

Shrub or *tree* to 3.5 m tall; twigs lanate, floccose or tomentose with mostly white, long-stalked, long-radiate, multangulate stellae, the midpoints reduced, sometimes armed with short, stout spines, their bases often tomentose. *Leaves* to 30 cm long, very variable in shape, broadly ovate, elliptical or obovate, the margins entire, sinuate-dentate or deeply pinnatifid, cordate to obtuse basally, above with scattered or dispersed mostly sessile, porrect stellae, beneath lanate with long stalked, porrect or multangulate hairs; petiole 2–5 cm long. *Inflorescence* several- to many-flowered, the peduncle lanate, usually branched 1–3 cm above the base, the racemes to 6 cm long; pedicels stout, thickening upwards, densely lanate, 1–1.5 cm long, slightly longer in fruit. *Flowers* sometimes showy, calyx 7–9 mm long, lobed halfway down, the lobes drying dark, filiform, splitting more deeply at the sinuses before corolla egress, not accrescent; corolla blue or mauve, to 3–5 cm across, lobed about halfway; anthers 11 mm long, tapering to a blunt tip; ovary with a few simple and stellate hairs on top, basal portion of the style with scattered simple hairs. *Fruits* 8–12 mm across.

This is a common species in the mountains of Chiriquí where it is usually distinctive with its blue or purplish flowers and whitish-lanate pubescence. It ranges from Mexico well into South America. In the mountains of Chiriquí there are some intergrades between this and S. *hispidum*, and in the lowlands of Chiriquí and the Azuero Peninsula there are occasional intergrades with S. *ochraceo-ferrugineum*. Plants suggestive of hybridization are marked with an asterisk in the citations below.

CHIRIQUÍ: Near F.S.U. cabin [Nueva Suisa], *Croat 13786* (MO). Beside Río Piedras E of Concepción, *D'Arcy 4235** (MO). Roadside between Nueva California and Río Chiriqui Viejo, *D'Arcy 4236* (MO). On bluff above Río Chiriqui Viejo near Nueva California, *D'Arcy 4242** (MO). Roadside, Nueva California, *D'Arcy 4247* (MO). Fence rows above Nueva Suisa, Volcán District, 6,000 ft, *D'Arcy 5332* (ADW, MO). Above Paseo la Canoa, 3,000 ft, *D'Arcy 5430** (MO). Boquete, 3,800 ft, Las Lagunas, 2 mi. SW of El Volcán, 4,200 ft, *Tyson 869** (FSU, MO). Nueva California, 4,000 ft, *Tyson 5694* (FSU, MO, SCZ). COLÓN: Isla Grande, *D'Arcy 4031** (MO).

13. **Solanum hayesii** Fern., Proc. Amer. Acad. Arts 35: 560. 1900. LECTOTYPE: Near Gatún, Dec. 1859, *Hayes s.n.* (GH, with label in hand of S. Hayes; GH, isotype, without Sutton Hayes label); paratype, *Fendler 246* (GH, MO).

Shrub or *tree* to 12 m tall; twigs velutinous to tomentose, drying with conspicuous furrows, rarely armed; trunk and large branches with short (5–10 mm long), stout spines. *Leaves* broadly elliptical, the margins entire or rarely sinuate or lobed, acute or obtuse apically, basally obtuse, often dimidiate, above glabrate drying blackish with scattered small, subsessile, multangulate hairs, beneath

velutinous to tomentose with long stalked stellae, appearing ochraceous when dry; petiole 1–6 cm long. *Inflorescence* several- to many-flowered, the peduncle velutinous, branched near the base or higher up, the racemes to 5 cm long with a conspicuous cicatrix from fallen flowers; pedicels 8–10 mm long, tightly pubescent with porrect stellae which have small but erect and conspicuous midpoints, elongating to 1.5–2 cm long and becoming apically stout in fruit. *Flowers* small; calyx 3–4 mm long, subtruncate, the lobes appearing as small umbos, splitting on corolla egress to near the base; corolla white, 10–12 mm across, lobed ¾ the way down; anthers 3 mm long, stout but tapering at the tip, opening by medium size pores; style pubescent near the base. *Fruit* globose, 10–15 cm across, often drying very wrinkled.

This species forms a large tree with spines on the trunk but not on the young parts. It is distinctive in its small flowers and usually shiny leaf uppersides. In mature plants the pubescence is usually brownish, but juveniles may have white pubescence. It ranges from Nicaragua to Peru.

BOCAS DEL TORO: Island of Bocas del Toro, *Durkee 71-134* (MO). Isla Colón, *Lao 98* (MO). Columbus Island, 3 mi. inland, *von Wedel 24* (MO, US). Isla Colón, *von Wedel 81* (GH, MO). Water Valley, near Chiriquí Lagoon, *von Wedel 1589, 1693* (both GH, MO, US). Old Bank Island, *von Wedel 1882, 2007* (both GH, MO, US). Isla Colón, *von Wedel 2845* (MO), *2980* (GH, MO, US). CANAL ZONE: Galen Point, *Blum & Dwyer 2141* (MO). Gamboa Navy Pipe Line along main dirt road, *Correa & Haines 527* (FSU, MO, PMA). Pipeline Road, 3.2 mi. NW of gate [Gamboa] *Croat 12750* (MO). Transisthmian Highway near Río Coco Solo bridge, *D'Arcy 5176* (BIRM, G, C, MO, UCWI). Fort Sherman site, U. S. Army Tropic Test Center, *Dwyer 7175* (MO, US). Chagres, *Fendler 246* (GH, MO). Near Gatún, *Hayes s.n.* (GH). Area W of Limon Bay, Gatún Locks and Gatún Lake, *Johnston 1723* (A, MO). Between Gatún and Lion Hill, *Pittier 2569* (NY, US). Camino al Fuerte San Lorenzo, después de Fort Sherman, *Quistgaard 16* (DUKE, MO). Gamboa, U. S. Navy Reserve, *Robyns 65-37* (MO, US). Fort Sherman on Peña Road, *Tyson & Ah Chu 1686* (MO). Between Fort Sherman & Fort San Lorenzo, *Tyson & Blum 3759* (MO). Barro Colorado Island, *Croat 6557* (F, MO), *7182* (DUKE), *7706* (DUKE, MO, NY), *8918, 8919, 9439, 9540* (all MO); *Shattuck 445, 828* (both MO, US); *Wetmore & Abbe 203* (A, F, GH, MO); *Woodworth & Vestal 379, 538, 608* (all A, F, MO); *s.n.* (MO). COCLÉ: Near El Valle, 600–1,000 m, *Allen 1203* (GH, MO, NY, US). Above El Valle 2 mi. on road to La Mesa, *Croat 13309* (MO). Flat, forested area below Cerro Pilón, *Croat 13441* (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, cloud forest, *Duke & Dwyer 13950* (MO). El Valle de Antón, 1,000–2,000 ft, edge of cloud forest and roadside, *Lewis et al. 2500* (DUKE, MO). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, *Porter et al. 4382* (MO); *4623* (DUKE, MO, NY). COLÓN: Lumber road on Santa Rita Ridge 2 mi. from highway, *Croat 13177* (MO). Santa Rita, zona de selvas altas perennifolias sobre suelos rojos lateriticos, arcillosos, secundaria, 200–300 m, *Gomez-Pompa et al. 2940, 2978* (both MO). Road from Pilón to Portobelo 1.2 mi. NE of Río Piedras bridge, *Nee & Mori 3658* (MO). Coast road from Portobelo to Pilón 2.9 mi. SW of Portobelo, *Nee & Mori 3667* (MO). Santa Rita Ridge 4–5.5 mi. E of Transisthmian Highway, advanced secondary forest, *Porter et al. 5250* (MO). PANAMÁ: One mi. W of Su Lin Motel along dirt road to Cerro Campana, 2,500 ft, *Correa & Dressler 362* (MO, PMA). Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 555* (DUKE, MO, PMA). Beyond Goofy Lake 2 mi. on road to Cerro Azul, *Croat 13011* (MO). Along road past Cerro Jefe toward La Eneida, *Croat 13081, 13098* (both MO). Cerro Jefe, *D'Arcy et al. 3961* (MO). Spoil bank near Río Bayano dam ca. 5 mi. S of Cañita, *D'Arcy 5190* (MO). Cerro Jefe, over-grazed pasture near entrance to Finca Indio, *D'Arcy 5226* (MO, MPU). Cerro Campana, *D'Arcy & Dressler 5490* (MO, P). Elfin forest beyond Motel Su Lin, Cerro Campana, 2,700–3,000 ft, *Duke 8645* (MO, OS), *8646* (MO). Cerro Azul, *Duke 9341* (MO, OS). Cerro Campana, ¾ way to summit from Pan American Highway, *Dwyer et al. 4729* (MO, PMA). Cerro Campana, *Hespenheide 2280* (MO). Road to Cerro Jefe 2–3 mi. S of Goofy Lake, 2,000–2,200 ft, *Lewis et al. 259, 260* (both GH, MO, US). Altos del Río Pacora, 2,500 ft, *Lewis et al. 2300* (MO). Cerro Campana, *Lewis et al.*

3082 (MO). Summit of Cerro Campana, *Porter 4897, 4973* (both MO). Cerro Azul, 2,000 ft, *Tyson 2172* (MO). Cerro Campana, W slope, 2,300 ft, *Tyson 4029* (MO). North of Cerro Azul 1 mi, 2,300 ft, *Tyson & Blum 4074* (MO). Cerro Azul between 2,000–2,300 ft, *Tyson 6397, 6405, 6406* (all FSU, MO). Cerro Campana, 2,000 ft, *Tyson 6438* (MO).

14. **Solanum hispidum** Pers., Syn. Pl. 1: 228. 1805. TYPE: Based on *S. stellatum* Ruiz & Pavon.

S. stellatum Ruiz & Pavon, Fl. Peru. 2: 40, *tab. 176, fig. b.* 1799, non Jacq., Coll. 3: 254, *tab. 5, fig. 2.* 1789. TYPE: (not seen).
S. scorpoideum Rusby, Descr. S. Amer. Pl. 113. 1920. TYPE: Colombia, *Smith 1144* (NY, US).
S. truncatum Standl. & Mort., Publ. Field Mus. Nat. Hist., Bot. ser. 18: 1095. 1938. TYPE: Costa Rica, *Standley 38760* (US).
S. pluviale Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 22: 104. 1940. TYPE: Panama, *Davidson 189* (F, MO, US).

Shrub or small *tree* to 7 m tall; twigs glabrescent, densely lanate to loosely tomentose with stalked porrect stellae, the midpoints often elongate and the stalks sometimes approaching bristles, armed or not with stout recurved often basally pubescent spines. *Leaves* to 25 cm long, broadly ovate or elliptical, pointed apically, basally obtuse to cordate, often dimidiate, the margins entire or usually with large, irregular-sinuate or angular lobes, above with dispersed to dense, sessile or subsessile porrect stellae, the midpoints often long and apically recurved, often scabridulous, beneath tomentulose with stalked stellae bearing reduced midpoints; petioles to 10 cm long, sometimes armed. *Inflorescence* many-flowered, the peduncle simple, forked or ternately branched, the unbranched portion usually less than 2.5 cm long, stout, densely tomentose, the racemes to 6 cm long and stout; pedicels stout, ca. 1.5 cm long, tomentose, sometimes glandular and sometimes with some simple hairs, becoming erect, stouter and longer in fruit. *Flowers* with the calyx 4–6 mm long, lobed partway down, the lobes linear and short, becoming larger and obtuse as the sinuses split, sinuses tomentose to glabrate; corolla white, 3–5 cm across, the lobes shallow; filaments 1–2 mm long, the anthers 6–9 mm long, slender, tapering to a small apex, dehiscing by small terminal pores and also longitudinally in the basal portion; ovary glabrate, sometimes tuberculate. *Fruit* 10–15 mm across, hard, mucilaginous.

This species stands out among other Panamanian species in the section by the gross appearance of the leaves, inflorescences, and flowers. The pubescence usually has an overall ferrugineous cast, but in some collections there may be whitish hairs like those of *S. hartwegii.* Some collections have darkened and glandular pedicels and calyces like those of *S. torvum.* In most features plants here considered to belong to this species display a much greater range of variation than is usual for other species in the genus.

In Panama, this species achieves the full expression of its morphology only in the Chiriquí mountains at middle and upper elevations, although occasional plants found at lower elevations show some features resembling *S. hispidum.* In the area around Concepción and on the road to the upland Volcán district, there appears to be large-scale hybridization with lowland *S. torvum* and *S. ochraceo-ferrugineum* and perhaps with the upland *S. hartwegii.*

CHIRIQUÍ: Near New Switzerland, central valley of Río Chiriquí Viejo, 1,800–2,000 m, *Allen 1421* (GH, MO, NY, US). Cerro Punta, in pasture S along road, *Croat 10433* (MO).

Cerro Punta along trail north, *Croat 10470* (MO). Between Bambito and Cerro Punta, *Croat 10609* (MO). Palo Santo, 3 mi. N of Volcán, *Croat 13553* (DUKE, F, MO, SCZ). Forested hill between Nueva Suisa and Cerro Punta, *Croat 13627* (MO). In draw between Río Chiriquí Viejo and Nueva California, *D'Arcy 4243* (MO). Nueva California, *D'Arcy 4250* (MO). Roadside 3 mi. N of Concepción, *D'Arcy 5303* (MO). Roadside 6 mi. N of Concepción, *D'Arcy 5304* (BIRM, C, F, MO). Ca. 2 mi. above Concepción, 3,250 ft, *D'Arcy 5306* (ADW, MO). In yard of "Sonrisa Chiricana," Nueva Suisa, 5,700 ft, Volcán District, *D'Arcy 5310* (MO). Above Cerro Punta, 7,600 ft, *D'Arcy 5350* (ADW, MO). Nueva California, ½ mi. S of Río Chiriquí Viejo, *D'Arcy 5364* (C, MO, PMA, UCWI). Above Cerro Punta, 6,300 ft, *D'Arcy 5373* (MO, MPU). Disturbed roadside area, Nueva California ca. 1 mi. S of Río Chiriquí Viejo, *D'Arcy 5382, 5383, 5384, 5385, 5386* (all MO). N side of Cerro Pando, 6,000 ft, *D'Arcy 5409* (F, MO). S side of Cerro Pando, 6,000 ft, *D'Arcy 5412, 5413* (both MO). Pan American Highway 7 mi. E of Río Gariche, W of Concepción, *D'Arcy 5423* (MO). Above Paseo la Canoa ca. 5 mi., 2,200 ft, *D'Arcy 5428* (MO, UCWI). Above Paseo la Canoa, 2,100 ft, *D'Arcy 5433* (MO). Ca. 1 mi. N of La Frontera, *D'Arcy 5435* (MO). Ca. 6 mi. S of El Hato de Volcán, 4,800 ft, *D'Arcy 5437* (MO). Above Boquete, *D'Arcy 5453* (MO). Roadside above Boquete, 4,800 ft, *D'Arcy 5455* (ADW, MO). In pasture above Boquete, 5,200 ft, *D'Arcy 5469* (MO, P). Rain forest, Bajo Chorro, Boquete District, 6,000 ft, *Davidson 189* (F, MO). Volcán Chiriquí, 8,500 ft, *Davidson 966* (A, MO). Cerro Horqueta NW of Boquete, 5,000–5,800 ft, *Dwyer et al. 446* (GH, MO, UC, US). Pastures around Boquete, 1,000–1,300 m, *Pittier 2907* (US). Near Cerro Punta, 6,800 ft, cloud forest and disturbed edge, *Ridgway & Solís 2388* (MO). Finca Collins, near Boquete, "El Velo," 6,150 ft, *Stern et al. 1968* (MO, US). 3 mi. S of El Volcán, 4,000 ft, *Tyson 874* (FSU, MO). Bambito, 5,000 ft, *Tyson 5637* (MO, SCZ). Nueva California, 4,000 ft, *Tyson 5692* (FSU, MO, SCZ). Valley of Upper Río Chiriquí Viejo, *White & White 94* (MO). Finca Lérida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 300* (GH, MO, US). Near Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 807* (GH, MO, NA).

15. **Solanum melongena** L., Sp. Pl. 186. 1753. LECTOTYPE: Herb. Linn. 248.28 (LINN; microfiche LINN 139: II. 2).

S. esculentum Dun., Hist. Sol. 208. 1813.

Large perennial *herb* to 60 cm tall; twigs loosely tomentose with whitish, sessile and stalked porrect stellae, sometimes glabrescent, rarely armed. *Leaves* large, to 25 cm long, ovate, pinnatifid-lobed to subentire, the margin sinuate, apically acute, basally cordate, truncate or narrowed, often dimidiate, above dispersed to densely pubescent with mostly sessile, porrect stellae, beneath more densely pubescent; the petioles to 6 cm long, loosely pubescent. *Inflorescence* a short, few-flowered, sessile or peduncled cincinnus, the first flowers functionally staminate, a few later flowers perfect; pedicels 1–2 cm long, tomentose, sometimes articulating near the base, longer and much stouter in fruit. *Flowers* with the calyx ca. 12 mm long, lobed about halfway, the lobes lanceolate, tomentose outside, glabrous within except at the tips, accrescent and splitting irregularly in fruit; corolla mauve, 3.5–5 cm across, lobed halfway with short teeth in the lobes; stamens free, the filaments 3–4 mm long, broader at the base, the anthers ca. 6 mm long, stout, dorsally flattened; ovary densely stellate on top, glabrescent, the style densely stellate below, less so above, the stigma of 2–4 small discoid lobes. *Fruit* very large, to 40 cm long, ellipsoid or ovoid with a thick rind and moist, firm pulp, purple-black (Panama), ultimately turning yellow, rose, green or brown.

This species is cultivated on a small scale in the Canal Zone and in Chiriquí. It is not known to occur in the wild in Panama. *Solanum melongena* is an im-

portant vegetable crop of the Old World. "Egg plant" (English), "Berengena" (Dominican Republic), "Pepino morado" (Antioquia).

CANAL ZONE: Cultivated by Chinese market gardeners near Curundu, *D'Arcy & Tyson 5484* (MO, SCZ).

16. **Solanum ochraceo-ferrugineum** (Dun.) Fern., Proc. Amer. Acad. Arts 35: 560. 1900.

S. *torvum* var. *ochraceo-ferrugineum* Dun. *in* DC., Prodr. 13(1): 260–261. 1852. LECTOTYPE: Mexico, *Berlandier 131* (G-DC, not seen; MO, isotype).
S. *fendleri* Heurck & Müll.-Arg., Obs. Bot. 130–133. 1881, non S. *fendleri* A. Gray, Amer. Jour. Arts & Sci., Ser. 2. 22: 285. 1856. TYPE: Panama, Canal Zone, Chagres, *Fendler 254* (GH, MO, US).
S. *isthmicum* Bitt., Fedde Rep. 11: 459 in obs, 1912. TYPE: Based on S. *fendleri* Heurck & Müll.-Arg.
S. *auctosepalum* Rusby, Descr. S. Amer. Pl. 114. 1920. TYPE: Colombia, *Smith 1150* (NY, US).
S. *diversifolium* Schlecht., Linnaea 19: 297. 1847, non S. *diversifolium* H. & B. *ex* Dun. Sol. Syn. 8. 1816. TYPE: Mexico, *Schiede & Deppe 1192*, non *1193* (MO).

Shrub or *tree* to 5 (–?12) m tall; twigs densely appressed-tomentose with sessile and stalked porrect stellae, the midpoints mostly much reduced and eglandular, the stalks multiseriate, armed with short, stout, straight or recurved spines which may be pubescent basally. *Leaves* to 15 cm long, broadly ovate, apically acute or acuminate, basally obtuse to cordate, often dimidiate, the margins sinuate, shallowly lobed, rarely entire, above sparsely to densely pubescent with sessile or stalked, porrect hairs, the midpoints mostly reduced; beneath as above but the hairs denser and stalks longer; petioles 1–5 cm long. *Inflorescence* lateral, mostly unarmed, several- to many-flowered, the peduncle densely appressed-tomentose, usually once branched 1–2 cm from the base, the racemes mostly 2–3 cm long; pedicels 1–1.5 cm long, sometimes becoming 2–2.5 cm long, erect and very stout in fruit, drying angled. *Flowers* with the calyx 10 mm long, the lobes 2 mm long and the sinuses splitting almost to the base during corolla egress, appressed-tomentose outside overall, rarely with a few glands, glabrous within except at the tips; corolla white, 2.5–5 cm across, shallowly lobed; anthers 4–7 mm long, slender, tapering to a fine-pointed apex, dehiscing by minute terminal pores and ultimately by longitudinal slits in the basal portion; ovary with a few simple glandular hairs and a few stellate hairs near the apex, the style glabrous, the stigma indistinctly lobed. *Fruit* 1–1.5 cm across, mucilaginous, yellow but seldom seen when mature; seeds yellow, much compressed, discoid, 2.5 mm across.

This species is much like S. *torvum* but is distinct in its thicker, densely pubescent, light-colored pedicels, in the overall pubescence of the calyx exterior, and in the absence of glands from these parts. There is often an orange or brownish cast to the emergent parts.

Solanum ochraceo-ferrugineum ranges from Mexico into South America but is replaced in the Antilles by S. *torvum*. It is the common lowland species of this group occurring as a weedy shrub or tree in Panama. In the Azuero Peninsula and in the lowlands at the base of the mountains of the Volcán district, this species

may have occasional glands on the inflorescence stellae, and occasionally pedicels or calyx are dark, very suggestive of the introgression from *S. torvum* which occurs in these areas. In the area around Concepción and along the road leading to the upland Volcán district, there is apparent hybridization between this species and *S. hispidum* and perhaps *S. hartwegii* as well. In other upland areas, however, plants of *S. ochraceo-ferrugineum* maintain the morphology of lowland populations.

Possible hybrids are identified in the collections below; those suggestive of *S. hispidum* with (+), those strongly suggestive of *S. torvum* with (**), and those only faintly suggestive of *S. torvum* with (*); presence of even one or two glands led to identification in this last category.

CANAL ZONE: Road K-6 E of Arraijan, *Croat 15033* (MO). Off Transisthmian Highway near Coco Solo Naval Hospital, *D'Arcy 5167* (GH, MO), *5168* (ADW, C, MO, MPU), *5175* (MO, UCWI). Drowned forest of Quebrada Culebra, *Dodge & Allen 17053* (MO). In government forest along Las Cruces Trail, *Hunter & Allen 695* (MO). N of island near bridge [island unknown], *White 90* (MO, US). Barro Colorado Island, *Aviles 55* (MO); *Wetmore & Abbe 176* (GH, MO); *Woodworth & Vestal 625* (GH, MO). CHIRIQUÍ: Between Concepción and El Hato de Volcán, *D'Arcy 4259, 4262* (both MO). Puerto Armuellas, *D'Arcy 4283*+ (MO). Ca. 1 mi. W of Las Lajas, *D'Arcy 5280*** (MO). Grassy roadside ca. 1 mi. W of Las Lajas, *D'Arcy 5281** (MO). Grassy roadside ca. 8 mi. W of Las Lajas, *D'Arcy 5282** (MO). Ca. 7 mi. W of Las Lajas, *D'Arcy 5285** (MO). Ca. 1 mi. W of San Lorenzo, *D'Arcy 5287*** (MO). Outskirts of David, grassy area, *D'Arcy 5290* (MO, NY), 5292 (MO). Ca. 3 mi. W of David, *D'Arcy 5294* (MO). Roadside 7 mi. W of David, *D'Arcy 5298** (MO). Roadside by Río Caimito, ca. 8 mi. W of David, *D'Arcy 5299** (MO). Roadside, Veladero, 800 ft, *D'Arcy 5479*** (MO). Boquete, Cerro Horqueta, 5,000–6,000 ft, *Dwyer & Hayden 7701*+ (MO). Pastures around Boquete, *Pittier 2959*+ (US). COCLÉ: East of Antón, *D'Arcy 4100* (MO). Penonomé, *D'Arcy 5274** (MO). Penonomé, *Dwyer 2011* (GH, MO). Río Grande, 10 mi. E of Nata, *Tyson 5273* (FSU, MO). Near Penonomé, *Williams 367** (US). COLÓN: Isla Grande, *D'Arcy 4033A*+ (MO). Corredo in abandoned helipad, *Duke 15204* (MO). DARIÉN: By cultivated field near junction Río Peresenico and Río Pirre, *D'Arcy 5520* (MO). HERRERA: Near Ocú, 100 m, *Allen 4051** (MO, US). 2 mi. S of Los Pozos, *Tyson 2700*** (MO). LOS SANTOS: Ca. 7 mi. S of Chitré, *D'Arcy & Croat 4176*** (MO). Loma Prieta, 800–900 m, *Duke 11876** (MO, WIS). Punta Mala, *Tyson 2718*** (MO). PANAMÁ: 3 mi. N of Buenos Aires, *Croat 14095* (MO). Roadside by bridge, 15 mi. E of Chepo, *D'Arcy 5185A, 5185B* (both MO). Roadside, 6 mi. E of Chepo, *D'Arcy 5186* (MO, P). Ca. 3 mi. W of Cañita, *D'Arcy 5186A* (MO). On spoil bank near Río Bayano dam ca. 5 mi. S of Cañita, *D'Arcy 5189* (MO, UCWI). Roadside ca. ½ mi. E of El Llano, *D'Arcy 5205* (MO). Roadside, Pan American Highway 1 mi. E of La Chorrera, *D'Arcy 5251* (MO). Ca. 3 mi. S of Capira, in grass pasture by stream, partial shade, *D'Arcy 5259* (MO). Roadside, Pan American Highway at Río Sajalices, *D'Arcy 5262** (MO, MPU). Cerro Jefe, *Duke 9417* (MO). Río Pacora (flooded 4 Nov. 1966), just below confluence with Río Corso, *Duke 12027* (MO, OS). Cleared area near highway 7 mi. W of Chepo, *Gentry & Tyson 1635* (MO). Along Río Pacora 1 km downstream from Carretera Interamericana, *Nee & Mori 3627* (MO). Cerro Jefe, E slope, 2,700 ft, *Tyson 3367* (MO, PMA), *3584* (MO). Ca. 1 mi. N of Cerro Azul, 2,300 ft, *Tyson & Blum 4073* (FSU, MO). Cañita, 18 mi. E of Chepo, *Tyson & Smith 4128* (FSU, MO). Cerro Azul, 2,000–2,300 ft, *Tyson 6404* (FSU, MO). Road to Cerro Campana, 1,500 ft, *Tyson 6424* (MO, SCZ). Las Sabanas, collector unknown, *1932* (MO, ex herb. Barro Colorado Island). SAN BLAS: Near Puerto Obaldía, *Croat 17002* (MO). Mulatuppu, *Duke 8534* (MO). Island of Soskatupu, only hill on island, 150 ft, *Kirkbride 181*+ (MO, NY). VERAGUAS: Just W of Santiago, *D'Arcy 5276** (MO). Ca. 2 mi. S of Cañazas, *Tyson 3706* (MO).

17. **Solanum subinerme** Jacq., Enum. Pl. Carib. 15. 1760; Sel. Stirp. Amer. 50, *tab. 40, fig. 3.* 1763; Sel. Stirp. Amer. Pict. 28, *tab. 259, fig. 15.* 1780–1. TYPE: ex herb. Jacquin (BM).

S. juripeba Rich., Act. Soc. Hist. Nat. Paris 1: 107. 1792. TYPE: French Guiana, *LeBlond s.n.* (C, ex herb. Rich.).
S. stamineum Steud., Flora 26: 764. 1848. TYPE: Surinam, *Hostmann & Kappler 1013* (MO).

Shrub or small *tree* to 4 m tall; twigs loosely pubescent with ochraceous, short-stalked porrect and multangulate stellae, armed with stout recurved spines to 5 mm long, glabrescent. *Leaves* to 15 cm long, ovate or elliptic, apically acute or acuminate, basally obtuse or rounded, mostly dimidiate, margins entire or usually repand, above with dispersed, nearly sessile porrect stellae which lack midpoints, beneath lightly tomentose with stalked, long-armed stellae, the midpoints wanting; petioles loosely tomentose, mostly unarmed; minor leaves often present. *Inflorescence* lateral, an unbranched raceme, the peduncles slender and remaining so, to 3 cm long; pedicels slender, 8–15 mm long, tomentulose, becoming thicker apically but not much longer in fruit. Flowers sometimes showy, slender and elongate; calyx 2–3 mm long with short, acicular lobes, not usually splitting at the sinuses in flower, finely-tomentose outside; corolla purple, lobed nearly to the base, the lobes 1.5–2 mm long, lanceolate, the median portion pubescent outside; stamens equal, the anthers narrowly lanceolate, coming to a fine apical point, 10 mm long, at first connivant but soon free, opening by minute terminal pores; style with stellate hairs along its length. *Fruit* a bright red or orange, juicy, globose berry 6–9 mm across.

This is a plentiful lowland species of disturbed habitats. It ranges very widely, from the Antilles and Mexico into South America; but in Panama, it has not been found west of Penonomé. There is considerable variation in the length of flower, but it is always slender and deeply lobed, and the purple corolla lobes are about as long as the anthers. The elongate nature of this flower is striking in mature bud.

CANAL ZONE: Along road K-15 in Empire Range, *Correa 518* (DUKE, MO, PMA). Roadside, Madden Forest, *Croat 8928* (MO). Roadside near Madden Wye, *Croat 12616* (MO). Pipeline Road 12.5 mi. NW of gate [Gamboa], *Croat 12767* (MO). Near beach, Fort Kobbe, *Duke 4192* (MO). Ancón Hill, *Duke 4576* (GH, MO), *4595* (GH, MO, US). Paraíso, hill opposite Paraíso Development, *Dwyer 7159* (MO). Frijoles, *Ebinger 321* (MO, US). Government forest along Las Cruces Trail, 75 m, *Hunter & Allen 667* (MO), *696* (MO, NY), *729* (MO). Summit road, *Jones 274* (MO). Ancón Hill, *Killip 3010* (MO). N of Frijoles, *Killip 3431* (MO). Madden Forest Preserve along Las Cruces Trail and highway, *Lewis et al. 5311* (MO). Pipeline road 16 mi. N of Gamboa, *Lewis et al. 5471* (MO). Around Culebra, *Pittier 2143* (MO, US). Balboa, *Standley 26090* (MO, US). Near Miraflores Locks, *Stern et al. 55* (GH, MO). Chiva Chiva Trail near Miraflores Lake, *Tyson et al. 1336* (MO, PMA). 2 mi. N of Cocoli, *Tyson 1631* (MO). One mi. N of Summit Garden, *Tyson & Blum 2000* (MO). Ancón Hill, *Williams 43* (NY, US). Fort Kobbe Road, *Woodson et al. 1419* (A, MO, NA, NY). Barro Colorado Island, *Croat 7479* (MO); *Zetek 5043* (MO). COCLÉ: Cerro Pilón, *Lallathin 120* (MO). PANAMÁ: Cerro Campana, dirt road 3 mi. from Interamerican Highway, *Correa & Dressler 384* (DUKE, MO, PMA). Roadside on way to Cerro Campana, *Croat 12019* (MO). Roadside, Cerro Jefe, *D'Arcy et al. 3964* (MO). Entrance to Finca Indio, Cerro Jefe, *D'Arcy 5225* (ADW, MO, WIS). Highway, 1 mi. E of La Chorrera, *D'Arcy 5252, 5254* (both MO). Ca. 5 mi. W of La Chorrera, *D'Arcy 5258* (MO). By airstrip near beach in Panama City, *Duke 4004* (MO). Road to Cerro Azul near Tocumen Airport, *Dwyer 2078* (MO). Tocumen Airport area, *Dwyer 3111* (MO). Tocumen to Cerro Azul on paved highway to Goofy Lake, *Dwyer 4073* (GH, MO). Tocumen, *Dwyer 4554, 4557* (both MO). Near Orange River, 3 mi. E of Juan Díaz, *Killip 3245* (MO, US). Grassland and savanna near Panama City airport, *Iltis & Iltis 1643* (MO, US, WIS). Southeast slope of Cerro Campana, *Lewis et al. 3121* (MO, UCWI). Near Cerro Jefe, 3,000 ft, *Lewis & Dressler 7578* (MO). Cerro Azul, *Porter et al. 4074* (MO). Between Pan American

Highway and Cerro Campana, *Porter et al. 4869* (MO). Cerro Azul, 2,000 ft, *Tyson 2055* (MO). Cerro Jefe, E slope, 2,700 ft, *Tyson 3415* (MO). Along road to Cerro Campana, 1,000 ft, *Tyson 6420* (SCZ). Thickets near Capira, *Woodson et al. 1299* (A, MO, NY). SAN BLAS: Mainland point opposite Isla Mosquito, *Duke 8991* (MO).

18. **Solanum torvum** Sw., Prodr. 47. 1788. TYPE: (not seen; Jamaica is the type locality).

S. ferrugineum Jacq., Hort. Schoenbr. 3: 46, *tab.* 334. 1798, ?1803. TYPE: (not seen).
S. ficifolium Ort., Nov. Pl. Hort. Matrit. 116. 1800, fide W. T. Stearn in litt. TYPE: (not seen).

Shrub or *tree* to 6 m tall; twigs tomentose with mostly stalked, porrect stellae, the midpoints much reduced and eglandular; armed with short straight or recurved spines which may be pubescent basally. *Leaves* to 25 cm long, broadly ovate, apically deltoid, basally obtuse or cordate, often dimidiate, the margins sinuate-dentate, above with dispersed stalked or sessile, porrect hairs, the midpoints as long as the radii or longer, beneath tomentose with mostly stalked, porrect hairs, the midpoints reduced, rarely armed on the veins; petioles 1–10 cm long. *Inflorescence* several- to many-flowered; peduncle tomentose, usually once-branched less than 1 cm from the base, the racemes mostly 1–2 cm long; pedicels 1–1.5 cm long, very slender, purple, drying dark, hispid-viscid with mostly glandular, simple hairs and some porrect stellae with long glandular midpoints, elongating and becoming stout in fruit. *Flowers* with the calyx purplish, 5 mm long, the lobes ca. 1 mm long and lengthening as the glabrous sinuses dehisce during corolla egress, viscid-hispid outside, glabrous within; corolla white, 1.5–3 cm across, shallowly lobed; filaments glabrous, the anthers 7–12 mm long, often oblique basally, tapering to a fine point and dehiscing by minute terminal pores; ovary with short, glandular, simple hairs near the apex, the style glandular-hairy near the base. *Fruit* a globose berry 1–1.5 cm across, glabrous, mucilaginous, erect, yellow, but seldom seen when mature; seeds flattened-discoid, 1.5–2 mm across.

This species is best recognized by its very slender, dark, glandular-pubescent pedicels, purple, glandular-pubescent calyx with glabrous sinuses, and the relatively fine even tomentum of the leaves which lacks an orange cast.

Solanum torvum is native to the Antilles but has been dispersed to many tropical regions in both New and Old Worlds. Many plants of Africa going under this name are reported to have red rather than yellow berries and may not be of the same species. In Panama, it has been collected in the lowlands of Bocas del Toro and on the Azuero Peninsula. In parts of the Azuero region this species appears to intergrade with populations of *S. ochraceo-ferrugineum*, and in the Volcán district, the characters by which *S. torvum* is easily recognized appear on plants which otherwise conform to *S. hispidum*.

BOCAS DEL TORO: Chiriquicito to 5 mi. S along Río Guarumo, rain forest by river, *Lewis et al. 1977* (MO, US). Isla Colón, *von Wedel 54* (MO). Water Valley, *von Wedel 658, 939* (both MO, US). CHIRIQUÍ: Above Boquete, 4,100 ft, by bridge over Río Cochea, *D'Arcy 5451* (MO), *5452* (F, MO). Francés Arriba School, 14 mi. N of David, 1,200 ft, scrub, *Lewis et al. 660* (MO). HERRERA: Near Ocú, open pasture, *Stern et al. 1710* (MO, US). Near Las Minas, rain forest type at La Peña, *Stern et al. 1768* (MO, US). South of Ocú 10

mi, *Tyson et al. 2833* (MO). LOS SANTOS: Roadside S of Macaracas, 1,100 ft, *Lewis et al. 1611* (GH, MO, US). Roadside between Tonosí & Macaracas, *Oliver et al. 3574* (MO).

F. Section **Acanthophora** Dun., Hist. Sol. 131–132. 1813. LECTOTYPE: *S. mammosum* L.

Herbs or *subshrubs*, pubescent with elongate, apparently simple hairs and often with short simple hairs and small stellae as well, mostly armed with straight, acicular, green to yellowish or orange spines. *Leaves* mostly broadly ovate, symmetrically palmately lobed, or sinuate dentate, often copiously armed and usually long pilose, membranaceous. *Inflorescence* few-flowered, lateral, a short, unbranched raceme, the first blossoms often staminate; calyx deeply lobed; stamens equal, the anthers elongate, gradually narrowed, opening by minute terminal pores; ovary glabrous. *Fruit* glabrous, fleshy, sometimes large, often with a large, dry seed chamber; seeds compressed, sometimes very flat with a conspicuous winged margin.

The apparently simple hairs of this section are its most distinctive feature. The long, uniseriate, multicelled hairs of mature plants are, from a developmental point of view, the elongate midpoints of sessile stellate hairs on which the radial arms have not developed and are referred to as derived simple hairs. The sequence leading to this is recapitulated on juvenile plants and sometimes on emerging leaves of mature plants.

Section *Acanthophora* is closely related to sect. *Lasiocarpa* from which it differs in the absence of stellate hairs on the ovaries and in the more general preponderance of derived simple hairs, as well as lighter overall construction of the plants, the stems being generally less stout and the leaves thinner. One species of sect. *Acanthophora*, *S. argillicolum* Dun. of the Guyanas, has small leaves and a scandent habit.

This section includes about a dozen species in tropical America and a few in Africa. *Solanum ciliatum* Lam. has become a pantropical weed. Most floras treat the weedy members of the section as either *S. aculeatissimum* Jacq. or *S. ciliatum* Lam. Neither of these species has been seen from Panama. The first seems to be a native of southern Africa and rarely if ever occurs in the New World. The second is the common species of Florida and the West Indies, rarely adventive in northerly parts of Central America.

Species of sect. *Acanthophora* are used in some countries for killing roaches and for a variety of medicinal purposes, and they are perhaps poisonous to mammals. Their armament is sufficient to discourage most grazing animals.

a. Flowers white, less than 1.2 cm across; spines mostly green to purple (live); pericarp less than 4 mm thick; fruits less than 2 cm across ..... 19. *S. acerosum*
aa. Flowers mauve, more than 1.5 cm across; spines mostly yellow or orange; pericarp more than 1 cm thick; fruits more than 3 cm across ..... 20. *S. mammosum*

19. **Solanum acerosum** Sendt. *in* Mart., Fl. Bras. 10: 61. 1846. TYPE: Brazil, *Sello s.n.* (P).—FIG. 21.

?*S. arcuatum* Sendt. *in* Mart., Fl. Bras. 10: 60. 1846. TYPE: Brazil, *Sello* (not seen).
?*S. stenandrum* Sendt. *in* Mart., Fl. Bras. 10: 68. 1846. TYPE: Brazil, *Pohl* (not seen).

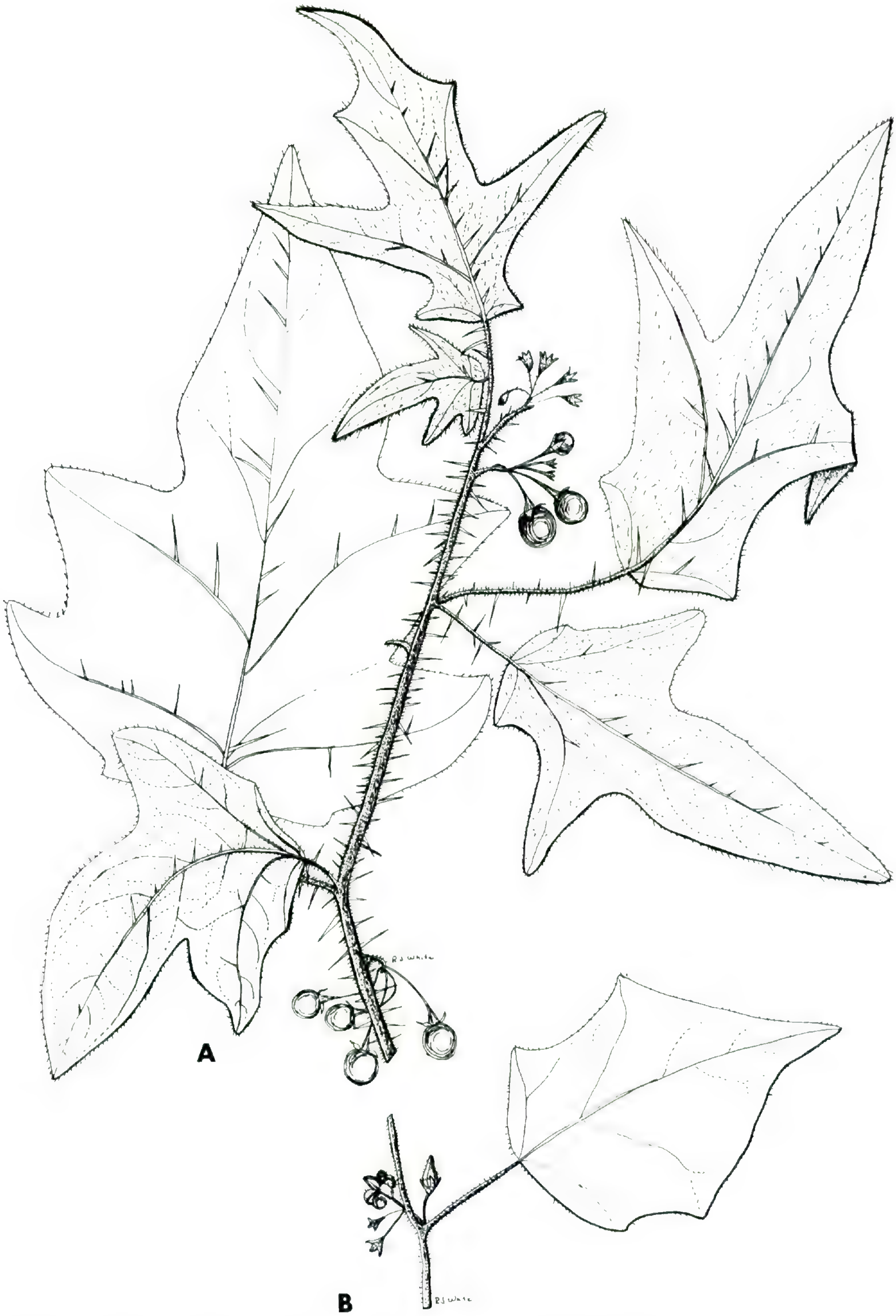

FIGURE 21. *Solanum acerosum* Sendt.—A. Fruiting branch (× ½). [After *Correa 1277* (MO).]—B. Flowers and leaf (× ½). [After *D'Arcy 6432* (MO).]

Herb to 1.5 m tall; twigs viscid-villous with simple hairs, copiously armed with acicular spines to 1.5 cm long which in age may become flattened and slightly curved but not strongly recurving. *Leaves* broadly ovate or elliptic, almost squarrose, deeply 3–9-lobed, the lobes mostly deltoid, the leaf base truncate to deeply cordate, both sides viscid-villous with long simple glandular hairs and tiny, scattered, sessile or stalked stellae on the margin and underside, copiously armed with acicular spines to 2 cm long; petioles to 12 cm long, copiously armed. *Inflorescence* a subumbellate raceme; peduncle short (to 10 mm long), villous, becoming stout and 1.5 cm long in fruits; pedicels 10 mm long, slender, armed, thickening in the upper portion and becoming 2.5 mm long in fruit. *Flowers* with the calyx 2–4 mm long, deeply lobed, the lobes elongate, narrow; corolla greenish-yellow or brownish-yellow, 1.5–2 cm across, lobed slightly more than halfway down; stamens connivent but not coherent, forming a narrow cone, the anthers 5 mm long, tapering evenly to a point, opening by tiny terminal pores subtended on each side by relatively large lips and occupying the entire width of the anther top. *Fruit* globose, shiny, viscid, green-striped and ripening black; seeds very much flattened with a broad winged margin, 3–4 mm in diameter.

This species is extremely spiny, the spines mostly straight, slender, greenish but drying yellowish or orange, often purple on the tips. The small white flowers, erect habit and viscid pubescence are also distinctive.

Selection of the correct name for this species posed a considerable problem, and not all aspects were satisfactorily resolved. During study of the group, types of a number of earlier names were examined and discarded[37] as inappropriate, but intensive study of the section over its full range will be necessary to determine the limits of the several morphological segregates (?species) and to select correct names.

Solanum acerosum is widespread; it has been collected from Honduras and

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[37] The following prior names, all applying to plants similar to S. *acerosum*, were rejected:

Solanum aculeatissimum Jacq., Coll. 1: 100, Ic. Pl. Rar. 1, *tab. 41.* 1786. TYPE: *Jacquin s.n.* (W).—This species has smaller, acuminate leaf lobes and a layer of fine simple hairs on the stem and leaves in addition to the coarse simple hairs of S. *acerosum.*

S. *ciliatum* Lam., Tab. Encycl., Supp. 2. 21. 1794. TYPE: Herb. *Lamarck, s.n.* (P).—This species has only coarse simple hairs, no fine hairs or stellate hairs on mature parts.

S. *incarceratum* R. & P., Fl. Peru. Prodr. 2: 40, *tab. 176.* 1794. TYPE: Herb. *Pavon, s.n.* (MA).—This species has fine simple hairs as well as coarse ones on the leaf uppersides; on the leaf undersides the pubescence is denser than on most S. *acerosum* and the leaf lobing is different. The calyx is also different.

S. *myriacanthum* Dun., Hist. Sol. 218, *tab. 19.* 1813. TYPE: *ex* Hort. *Monsp. s.n.* (MPU).—The leaf undersides are covered with dense minute hairs, scattered, stalked stellae, and on the leaf uppersides there is a mixture of minute and coarse simple hairs.

S. *acerifolium* H. & B. *ex* Dun., Sol. Syn. 41. 1816.—Authentic material labelled by Dunal seen at Paris (P). The leaf undersides are pilose with coarse simple hairs and widely scattered small stellae.

S. *quinquangulare* Willd. *ex* R. & S. *in* L., Syst. Veg. 4: 669. 1819. TYPE: Venezuela, *Bredemeyer* (not seen).

S. *reflexum* Schrank, Pl. Rar. *tab. 81.* 1822. TYPE: (not seen).

S. *atropurpureum* Schrank, Syll. Pl. Nov. Ratisb. 200. 1824. TYPE: *Schrank, s.n.* (M).—The leaf lamina is glabrous.

S. *vernicatum* Lindl., Bot. Reg. Misc. 74 [137]. 1838. TYPE: (not seen).

Costa Rica to Colombia and Brazil and also from the Transvaal. No specimens have been seen from the Antilles. In Chiriquí it is a frequent plant at middle and upper elevations in cafetals, pastures and even in cloud forests.

CHIRIQUÍ: Near "New Switzerland," central valley of Río Chiriquí Viejo, 1,800–2,000 m, *Allen 1366* (F, MO). Wet roadside, Río Chiriquí Viejo above Nueva California, *D'Arcy 4240* (MO). In cafetal, Los Naranjos, *D'Arcy 4269* (MO). In vegetable field above Nueva Suisa, Volcán district, 6,000 ft, *D'Arcy 5327* (MO). South side of Cerro Pando, 6,000 ft, plentiful in abandoned cultivation, *D'Arcy 5396* (MO). North side of Cerro Pando, low weed area, *D'Arcy 5405* (MO). In cafetal above Boquete, 4,800 ft, *D'Arcy 5457* (MO). Bajo Chorro, Boquete district, 6,000 ft, rain forest, *Davidson 449* (GH, MO, US). Cerro Horqueta, 1,500 m, *Duke et al. 13663* (MO). Boquete, Finca Collins, 5,000 ft, dense woodland, *Dwyer & Hayden 7680* (MO, US). Boquete, Cerro Horqueta, 5,000–6,000 ft, dense woodland in cloud forest, *Dwyer & Hayden 7742* (MO). Cerro Horqueta, 4,500–5,500 m, rain forest, *Dwyer & Lallathin 8735* (MO). Boquete, Finca Collins, "El Velo," 6,150 ft, *Stern et al. 1987* (MO, US). Finca Lérida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 290* (MO). Near Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 938* (GH, MO). Between Bambito and La Amenaza, *Correa 1277* (MO).

20. **Solanum mammosum** L., Sp. Pl. 187. 1753. TYPE: (not seen).

Herb or *shrub* to 1.5 m tall; twigs viscid-villous with long simple hairs, armed with yellow or green, acicular spines which in age become flattened, recurved, woody, 2.5 cm long; stems fistulose. *Leaves* 6–20 cm long, broadly ovate, pinnatifidly lobed, the base truncate to deeply cordate, both sides villous with long, simple, glandular hairs, short-stalked glands and sessile, long-radiate stellae with ascending radii, armed with flattened acicular spines to 3 cm long; petioles 3–7 cm long, sparingly armed. *Inflorescence* lateral, several-flowered, a short raceme on a short (to 10 mm long) peduncle; pedicels 5–12 mm long, becoming stout and somewhat longer in fruit, viscid-villous to lanate, armed or not. *Flowers* with the calyx unarmed, deeply lobed, the lobes lanceolate, pubescent outside, 3–6 mm long; corolla violet, showy, exceeding the calyx 2–3 times in bud, 3–4 cm across, lobed about halfway; filaments very short, the anthers 10–12 mm long, linear-oblong and tapering. *Fruit* orange or yellow, 4–7 mm long, ovoid, often with a 2 cm long, nipple-like apex, and sometimes bearing one or more nipple-like protrusions at the base; seeds compressed-lenticular, 5–7 mm across, not winged, finely rugose, shiny.

This species is one of the most densely pubescent of all Panamanian species of *Solanum*. The acicular spines and unusual fruit shape help distinguish it from other species.

Solanum mammosum is cultivated for ornament and household use in many parts of the American tropics. In Panama it is cultivated and apparently also grows wild. It is used in some countries for killing roaches and in Darién for "extraction of maggots" (Duke). "Nipple fruit" (English), "Moza" (Cuña), "Tetilla" (Darién), "Teta de China" (Panamanian Spanish).

CHIRIQUÍ: Tolé, *Tyson et al. 4225* (MO). DARIÉN: Río Pirre, *Duke & Bristan 8276* (MO, OS). Along the Sambú River above tide limit, *Pittier 5552* (US). PANAMÁ: Piria, 150 m, cultivated, *Duke 14408* (MO, WIS). Panamá Golf Club, *Piper 5851* (US). Chepo, 60 m, *Pittier 4446* (US). Las Sabanas, roadside, *Standley 25840* (US). Near Juan Franco Race Track, in marsh, *Standley 27804* (US). Nueva San Francisco, savanna, *Standley 30702* (US). Río Tapia, in grassland, *Standley 41180* (US). La Chorrera, *Zetek 3914* (MO).

Subgenus **Brevantherum** (Seithe) D'Arcy, Ann. Missouri Bot. Gard. 59: 267. 1972 [1973].

Sect. *Brevantherum* Seithe, Bot. Jahrb. Syst. 81: 297. 1962. TYPE: S. *verbascifolium* sensu auct., non L. (= S. *erianthum* D. Don).

Shrubs, *trees* or *vines*, unarmed, pubescent with variously branched or stellate hairs. *Leaves* entire or nearly so. *Inflorescence* various, opposite the leaves or lateral, often appearing terminal and sometimes situated at a dichotomy of the stem; pedicels deciduous at the base or above. *Flowers* small to medium-sized; calyx hardly accrescent in fruit; corolla deeply or shallowly lobed; anthers stout, opening by large terminal pores and sometimes ultimately by longitudinal slits which are not particular to the basal portion; ovary glabrous to tomentose. *Fruit* mostly globose, often pubescent; seeds flattened.

Subgenus *Brevantherum* embraces those sections of the genus with branched or stellate hairs which by their stout anther shape and mode of dehiscence and their fundamental lack of armament are not satisfactorily placed in subg. *Leptostemonum*. The majority of species has entire or nearly entire leaves.

Members of sect. *Brevantherum* show some similarities in branching pattern and fruit shape to the subgenera *Bassovia* and *Archaesolanum* (not in Panama) and these species, *e.g.* S. *abutiloides* (Griseb.) Bitt. & Lillo of Argentina, may represent a relict morphology from which other sections in the subgenus have evolved. Subgenus *Solanum* and subg. *Leptostemonum*, with which these sections have been variously allied by different workers, were probably evolved in different lineages.

In Panama, this subgenus is represented by sections *Brevantherum*, *Extensum*, *Holophylla*, *Lepidota*, and *Pseudo-capsica*.

G. Section **Pseudo-capsica** R. & S. *in* L., Syst. Veg. 4: 569, 584. 1819. TYPE: S. *pseudocapsicum* L.

Unarmed *shrubs* or *trees*, rarely scandent, glabrate or pubescent with simple or branched hairs; the stems often angled, occasionally sarmentose. *Leaves* simple, entire or sparingly lobed, ovate to linear, sometimes fleshy. *Inflorescence* single- or few-flowered, terminal or nearly so and becoming lateral or leaf-opposed, the peduncle short or absent. *Flowers* with the calyces prominently lobed, somewhat accrescent; corolla stellate, mauve or white, small, less than 2 cm across; stamens equal, the filaments glabrous, the anthers often connivent but not connate, dehiscing by 2 large, introrse apical pores and sometimes ultimately longitudinally by longitudinal slits; ovary glabrous or pubescent. *Fruits* conspicuous, mostly red, orange or yellow, fleshy; seeds compressed, small.

This small group with fewer than a dozen species is more typical of drier regions of the world than Panama. Most species are from Mexico or from extratropical South America. *Solanum pseudocapsicum* is widely cultivated for ornament in temperate regions. Species of this section are similar to the genus *Capsicum* in the type of inflorescence, the appearance of fruits and seeds, and the alkaloid chemistry, but there may not be a close relationship.

21. **Solanum pseudocapsicum** L., Sp. Pl. 184. 1753. LECTOTYPE: Madeira, Herb. Linn. 248-4 (LINN).

Erect, glabrate *shrub* to 2 m tall; stem terete or slightly angled, puberulent with small dendritic hairs or glabrous. *Leaves* entire or faintly sinuate, narrowly elliptic or oblanceolate, apically acuminate or obtuse, basally narrowed, dark green above, lighter beneath, glabrous or with a few forward-curved hairs on the midrib and margins, the midrib prominent beneath; pedicels 3–10 mm long, slender but thickening in fruit. *Flowers* with the calyx 4–6 mm long, the lobes deltoid to narrowly oblong with obtuse or rounded, fine ciliate tips, the midvein evident; corolla 1–1.5 mm across, sometimes reflexed, white, deeply-lobed; stamens spreading or connivent in a tube, the filaments glabrous, stout, 1 mm long, the anthers 2.5–3 mm long, stout; style filiform, straight. *Fruit* an orange-red berry, 12–18 mm across, shiny and conspicuous, the stylar scar evident; seeds compressed-lenticular, shiny.

Known in Panama only as a plant cultivated for ornament, it has been recently introduced to the Volcán district. It has no common name. "Jerusalem cherry" (English).

CHIRIQUÍ: Cultivated, Nueva Suisa, Volcán District, 6,000 ft, *D'Arcy 5418* (MO).

H. Section **Lepidota** (Dun.) Seithe, Bot. Jahrb. Syst. 81: 298. 1962.

Sect. *Pachystemonum* subseries *Lepidota* Dun. *in* DC., Prodr. 13(1): 29, 131–137. 1852. TYPE: S. *lepidotum* Dun.

Shrubs or *trees*, pubescent mainly with scutellate hairs (stellate hairs, the radial arms of which are laterally fused to form a peltate disc). *Leaves* entire, moderate-sized, petiolate; minor leaves often present. *Inflorescence* becoming lateral or opposite the leaves, an erect, long-stalked corymb, remaining erect in fruit, the peduncle unbranched for most of its length, then branched; pedicels short and angled, articulating at the base. *Flowers* small, congested; calyx prefloration complete, splitting longitudinally ⅔ the way down into 3–5 subequal acute or obtuse lobes; corolla white, irregularly lobed, pubescent outside; stamens equal, the anthers short, stout, dehiscing by large terminal pores and longitudinally; ovary conical, glabrous. *Fruit* a globose berry.

This section is distinguished by the scutellate hairs which provide a fine, smooth covering over most parts of the plant. The complete closure of the calyx in bud is unusual in the genus. The appearance of the inflorescence is very suggestive of sect. *Brevantherum*, although it is situated laterally on the stem or opposite the leaves and not at a dichotomy of the stem. If it is in fact related to S. *blodgettii* Chapm. of Florida or to S. *punctulatum* Dun. of Jamaica, then this section would be better placed in subgenus *Leptostemonum*, for these two species occasionally produce spines.

The section ranges from Argentina to the Greater Antilles. Many species have been described, but many of these are probably synonymous with the single species included here. In Central America, there may be only one species.

22. **Solanum argenteum** Dun. *ex* Poir. *in* Lam., Encycl. Supp. 3: 755. 1814. TYPE: Brazil, *Dombey, s.n.* (P-Juss.).

S. *lepidotum* Dun., Sol. Syn. 17. 1816. TYPE: Colombia, *Bonpland, s.n.* (P).
S. *celsum* Standl. & Mort., Publ. Field Mus. Nat. Hist., Bot. ser. 18: 1077. 1938. TYPE: Costa Rica, *Skutch 2364* (GH, MO, NY).

Shrub to 7 m tall; twigs slender, pubescent with sessile, scutellate hairs with midpoints reduced or absent. *Leaves* to 20 cm long, ovate, apically acuminate, basally rounded, glabrate above, beneath vestite with sessile, crowded scutellate hairs and a mixture of porrect, pauciradiate hairs; petioles to 1 cm long; minor leaves mostly wanting. *Inflorescence* a congested, small corymb standing erect, almost terminal or becoming lateral or opposite the leaves, the peduncle slender, to 10 cm long, vestite with a yellowish or bronzy cast, angled near the apex; pedicels to 5 mm long, angled, becoming 8–10 mm long, stouter and dark in fruit. *Flowers* small; calyx irregularly lobed about halfway down, vestite outside, glabrous within, slightly accrescent in fruit; corolla white, 6–8 mm across, vestite outside, drying testaceous, glabrous within; filaments basally connate, glabrous, the anthers 2 mm long, stout; ovary sometimes with a few scutellate hairs on top, glabrous on the sides, the style glabrate. *Fruit* 6–8 mm across, glabrate, ripening black.

This species is commonly confused with S. *schlechtendalianum* Walp., but that species lacks scutellate hairs. *Solanum argenteum* occurs in forests at low and middle elevations.

The name S. *argenteum* is here employed in a wide sense to include plants ranging from Brazil to Mexico and as such probably embraces a number of infraspecific taxa, the limits of which are not clear. Plants from Central America usually have a greyish or silvery cast to the leaf pubescence, and their hairs range from scutellate to porrect and multiradiate on the same leaf. The leaf base is usually rounded or obtuse. Many plants from South America, including the type collection, have pubescence of a brownish cast, and the hairs are all scutellate, but some collections, including type collections of several varieties described from Brazil, closely resemble Panamanian material as to pubescence. Most South American material has basally acuminate or acute leaves, but leaf bases appear to exhibit a continuous range of shape. Type material seen of S. *lepidotum* is like that of S. *argenteum*. The type collection of S. *celsum* is representative of Central American material, but until the limits of S. *argenteum* and its infraspecific taxa can be clarified, it is preferable to use the earlier name.

CANAL ZONE: Barro Colorado Island, *Foster 1711* (MO). 1–3 mi. from Gorgona, 40–150 m, along old trail above the reservoir, *Maxon 4745* (GH, MO, NY). Between France Field and Cativál, wooded swamp, *Standley 30374* (MO, US). Barro Colorado Island, *Wetmore & Abbe 200* (A, GH, MO). CHIRIQUÍ: Chiriquí Viejo Valley, *White 92* (GH, MO, US). Near El Volcán, *White 224* (MO). COCLÉ: Between Cerro Pilón and El Valle de Antón, 700–900 m, cloud forest, *Duke & Dwyer 13955* (MO). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7927* (MO). DARIÉN: 0–2 mi. E of Tres Bocas along shortest headwater of Río Cuasi, premontane rain forest, *Kirkbride & Duke 1181* (MO). Cana-Cuasi Trail, Chepigana district, 2,000 ft, *Terry & Terry 1498* (A, F, MO). PANAMÁ: Cerro Azul, 2,000 ft, *Dwyer 2064* (MO). Cerro Jefe, summit, 2,900 ft, *Dwyer et al. 7262* (MO). Goofy Lake to 1.5 mi. S, 1,800 ft, roadside thicket, *Dwyer & Hayden 8046* (MO). NE slope of Cerro Jefe on road to Buenos Aires, 2,600 ft, *Tyson et al. 3251* (MO, SCZ).

I. Section **Brevantherum** Seithe, Bot. Jahrb. Syst. 81: 297. 1962. TYPE: S. *verbascifolium* sensu auct., non L. (= S. *erianthum* D. Don).

Cliocarpus Miers, Ann. Mag. Nat. Hist., Ser. 2. 4: 141. 1849. TYPE: *C. gardneri* Miers (= *Solanum* sp.).

Unarmed *shrubs* or *trees* to 12 m tall, mostly tomentose or scabrous, with a variety of stalked, or sessile, porrect, dendritic or echinoid hairs, the stalks sometimes long and multiseriate, often foetid. *Leaves* entire, often tomentose beneath, petiolate; minor leaves often present. *Inflorescence* terminal or subterminal mostly at a dichotomy of the stem, a panicle or corymb standing above the foliage on an elongate, erect, branched peduncle bearing short racemes and mostly short pedicels; fruits usually held erect. *Flowers* sometimes showy, medium-sized; calyx cupular, occasionally swollen at the base; corolla mostly densely tomentose outside, white or blue; stamens equal, the anthers stout, elongate or elliptical, opening by large terminal introrse pores; ovary mostly somewhat pubescent. *Fruit* globose, sometimes pubescent; seeds small, compressed-lenticular.

This section includes several dozen species occurring in the American tropics and at least one species in the Old World. Several species have become widespread weeds. They are mostly plants of disturbed lowland habitats, although S. *umbellatum* ranges to over 2,000 m in Panama.

Useful references:

Roe, K. E. A revision of *Solanum* sect. *Brevantherum* in North and Central America. Brittonia 19: 353–373. 1967.

———. A revision of *Solanum* section *Brevantherum* (Solanaceae). Brittonia 24: 239–278. 1972.

a. Hairs on the leaf undersides sessile, the rays porrect and flat against the lamina; base of the calyx glabrate and often drying dark; leaf base attenuate; calyx lobed halfway down ..... 26. S. *rugosum*

aa. Hairs on the leaf undersides mostly stalked, the rays flat against the lamina or not, base of the calyx not drying dark, mostly pubescent; leaf bases various; calyx variously lobed.

b. Calyx lobed halfway down; ovary densely tomentose; hairs of twigs drying with a yellow to brownish cast.

c. Leaves lanceolate, the base attenuate, scabrous, drying bright, shiny green or brown above ..... 23. S. *asperum*

cc. Leaves ovate or elliptic, the base not attenuate, felty, drying dull on both sides ..... 24. S. *erianthum*

bb. Calyx lobed much more than halfway down; ovary sparingly pubescent; hairs drying whitish to yellowish.

d. Calyx with a swollen cupule at the base, the lobes tomentose within; pubescence of twigs mostly of minute, pulverulent, sessile stellae .. 25. S. *hazenii*

dd. Calyx not swollen at the base, the lobes glabrous within; pubescence of twigs and inflorescences of long-stalked, shaggy stellae .... 27. S. *umbellatum*

23. **Solanum asperum** L.-Cl. Rich., Act. Soc. Hist. Nat. Paris 1: 107. 1792. TYPE: French Guiana, *Leblond s.n.* (P).

S. *salviifolium* Lam., Encycl. Meth. 2: 14. 1793. TYPE: Herb. *Lamarck s.n.* (P).
S. *radula* Vahl, Eclog. Amer. 2: 16. 1798. TYPE: Surinam, *Rohr 54* (C; MO, photo; IDC 2201. 72: I. 5).

Shrub or *tree* to 7 m tall; twigs pulverulent-tomentose with small, pauciradiate stellae which have a yellowish or brownish cast. *Leaves* to 15 cm long and 4 cm broad, lanceolate or narrowly elliptic, acuminate at each end, margins slightly revolute, above bright, dark green, shiny, scabrous with dispersed, sessile, porrect stellae, beneath tomentose with stalked porrect stellae; petiole very short, merging gradually into the elongate leaf base; minor leaves wanting. *Inflorescence* a long-stalked cyme standing well above the foliage, the peduncle 5–12 cm long, branching near the apex, densely pulverulent-tomentose with mostly porrect stellae; pedicels 2–5 mm long, angled, articulating in fruit at about the middle, tomentose, drying with sharp angles. *Flowers* small, white, drying yellow; calyx 1 cm across, deeply lobed; filaments glabrous, the anthers 3 mm long; ovary and lower portion of the style tomentose. *Fruits* 8–10 mm across, pubescent; seeds 1.5–2 mm across.

This species is recognizable by the narrow leaves which are usually shiny and scabrous above. The absence of echinoid or of coarsely stalked stellae and the mostly stalked hairs on the leaf undersides are also important characters.

This species occurs in forest openings and second growth thickets of lower to middle elevations from British Honduras to Brazil.

CANAL ZONE: Barro Colorado Island, end of Harvard Trail, *Croat 4266* (MO). Barro Colorado Island, shoreline of Miller Peninsula SW of Orchid Isle, *Croat 6359* (MO). Pipeline road, 10 mi. NW of gate, *Croat 12775* (MO). Barro Colorado Island, rear No. 8 lighthouse clearing, *Croat 12839* (MO). Gatún Station, Panama Railroad, *Hayes 195* (NY). Thickets along Panamá-Cruces Trail, 25 m, *Killip 3253* (MO, US). Pipeline Road between 0–3.5 mi. NW of Gamboa, rain forest, *Lewis & Sharp 3* (MO). Vicinity of Contractor's Hill along K-2 road, edge of secondary rain forest, *Lewis et al. 2876* (DUKE, MO). Navy reservation N of Gamboa, *Robyns 65-53* (MO, US). Barro Colorado Island, *Miller 21*, *Shattuck 48* (MO). Barro Colorado Island, Banana clearing near dock, *Shattuck 729* (MO). Barro Colorado Island, shore N end of Chapman Trail, *Woodworth & Vestal 517* (GH, MO). COCLÉ: Cerro Pilón, *Lallathin 119* (MO, PMA). COLÓN: Vicinity of Camp Piña, 25 m, *Allen 3677* (C, GH, MO, NY, US). Santa Rita en zona de selvas altas perennifolias sobre suelos rojos lateriticos, arcillosos, 200–300 m, *Gomez-Pompa et al. 3100* (MO). Santa Rita Ridge, 4–4.5 mi. E of Transisthmian Highway, advanced secondary forest, *Lewis et al. 5268* (MO, NY; not DUKE, = *S. rugosum*), 5278 (MO). DARIÉN: Camp Tiotuma, helipad in premontane rain forest, 164 ft, *Duke 15513* (WIS). PANAMÁ: 5 mi. N of Cerro Azul on road to Cerro Jefe, 2,400 ft, *Blum et al. 1746* (FSU). Beyond Goofy Lake on road to Cerro Jefe, *Correa & Dressler 452* (DUKE, MO, PMA). 2 mi. beyond Goofy Lake on road to Cerro Azul, *Croat 13019* (MO, left hand specimen only). 6 mi. E of Chepo on Pan American Highway, *Duke 4070* (MO). Halfway between El Llano and Río Mamoni, *Duke 5598* (GH, MO). Cerro Campana, forest bordering grasslands, *Duke 8688* (DUKE, MO, US). Cerro Azul, *Duke 9348* (MO). Cerro Azul, 2,000 ft, *Dwyer 2079* (GH, MO, NY). Cerro Jefe, *Dwyer 8478* (ADW, MO, MPU). La Campana, Cerro Campana, in low shrubby area in grassland on top of mountain, *Ebinger 378* (MO, US). Near Goofy Lake, forest, *Ebinger 991* (MO). Cerro Azul, selva alta perennifolia, *Gomez-Pompa et al. 3426* (MO). 2–3 mi. S of Goofy Lake, road to Cerro Jefe, 2,000–2,200 ft, lower elevations of cloud forest, *Lewis et al. 240* (GH, MO, NY). 1 mi. N of Goofy Lake, edge of cultivated field, *Oliver et al. 2678* (MO). Cerro Azul, in sun, 2,000 ft, *Tyson 2174* (FSU, MO). Cerro Campana, W slope, 2,500 ft, *Tyson et al. 2330* (FSU). NE slope Cerro Jefe on road to Buenos Aires, 2,600 ft, *Tyson et al. 3259* (MO).

24. **Solanum erianthum** D. Don, Prodr. Fl. Nepal. 96. 1825. TYPE: Nepal, *Wall. Herb. 2616c* (K, not seen).

S. *verbascifolium* sensu auct., non L., Sp. Pl. 184. 1753.

Shrub or *tree* to 10 m tall; twigs terete or flattened, drying with angles or grooves, tomentose with variously stalked dendritic-echinoid and echinoid hairs, whitish or drying yellowish-brown, becoming floccose below. *Leaves* to 20 cm long, ovate to elliptic, apically acute or acuminate, basally acute, obtuse, rounded, sometimes oblique, thick and felty, above with dispersed to dense, mostly short-stalked, subechinoid stellae and scattered echinoid stellae, tomentose beneath with dense, long-stalked stellae; minor leaves absent. *Inflorescence* erect, mostly standing above the leaves, a condensed corymb or panicle, the peduncle 5–20 cm long with dense, mostly echinoid stellae; pedicels stout, 2–5 mm long, tomentose, articulating almost at the base. *Flowers* not showy, buds turbinoid (top-shaped); calyx 7–9 mm long, slightly accrescent in fruit, lobed about halfway down, the lobes obtuse-deltoid, densely tomentose outside and near the apex within; corolla white, drying brown, 1.5 cm across, deeply lobed, pubescent outside; filaments 2 mm long, broadened at the base, glabrous; the anthers 3 mm long; ovary densely stellate-tomentose, the style sparsely pubescent. *Fruits* 7–12 mm across, dull yellow, tomentose; seeds 1.5–2 mm long.

This species is distinctive in its thick, felty leaves, top-shaped flower buds, and the dense tomentum of the inflorescence, made up mostly of echinoid hairs.

This species has long been known erroneously as S. *verbascifolium* L., but Urban (Fedde Repert. 16: 32. 1920) and Roe (Taxon 17: 176. 1968) have shown, using different reasoning, that the name S. *erianthum* is correct.

The species is a nearly pantropical weed, growing widely in the Old World tropics and in the New World in the Antilles, Florida, Mexico, and parts of Central America. However, it hardly if at all penetrates into South America except in the Guianas and eastern Venezuela.

Solanum erianthum is included in the *Flora of Panama* with hesitation. Only one collection has been seen, and it may represent a waif or a mislabelling. The single collection was taken by Duchaissing, probably in the middle part of the last century and is labelled only "Panama" and "*Solanum verbascifolium* L." Duchaissing also collected in Barbados where S. *erianthum* is plentiful—he may have mixed his labels. The above description is taken from a range of specimens from Florida. The Duchaissing specimen is included within this range of morphology and appears quite similar to Florida plants.

WITHOUT LOCALITY: *Duchaissing, s.n.* (NY).

25. **Solanum hazenii** Britt., Bull. Torrey Bot. Club 48: 338. 1922. TYPE: Trinidad, *Britton & Hazen 156* (NY).—FIG. 22.

S. *verbascifolium* var. *viridi-scabrum* Dun. *in* DC., Prodr. 13(1): 115. 1852. TYPE: *Sieber 21* (MO).

Shrub or *tree* to 10 m tall; twigs pulverulent with very fine, almost granular, echinoid hairs, often with a yellowish cast. *Leaves* large, to 50 cm long and 40 cm broad, broadly ovate or elliptical, short-acuminate apically, rounded or short-acuminate basally, above scabridulous with tiny, dispersed, sessile stellae, beneath fine-tomentose with larger (still small) stalked stellae; petioles 4–12 cm long; minor leaves mostly wanting. *Inflorescence* a long stalked cyme standing well

FIGURE 22. *Solanum hazenii* Britt., branch in flower and young fruit (× ½). [After *D'Arcy 4049* (MO).]

above the foliage, the peduncles stout, 8–12 cm long, branching near the top, finely tomentose; pedicels 1–5 cm long, slender, drying angled, articulating at the base, pubescent. *Flowers* often showy; calyx 3–5 mm long with a conspicuous swollen ring or ferrule at the base, lobed to the base, finely pubescent outside and

in, the hairs minute, porrect, multangulate; corolla white, drying brownish yellow, 8–14 mm across, lobed about halfway down; filaments glabrous, the anthers 3 mm long; ovary glabrate to tomentose, the style glabrous. *Fruits* 8–11 mm across, yellow, glabrescent; seeds 1.5–2 mm across.

Distinctive in its minute pubescence, *S. hazenii* may be recognized also by the unusual annular thickening at the base of the calyx.

This species occurs on roadsides and in forest openings in lowlands from central Mexico to Colombia and Trinidad.

CANAL ZONE: Road C-16, NW of Pedro Miguel, *Croat 12256* (SCZ). Boy Scout Road, Madden Dam area, second growth forest, *Porter et al. 4049* (DUKE, MO). Boy Scout Camp on Madden Lake, *Tyson 5450* (MO). COLÓN: Near Giral near bat cave, *Blum & Tyson 522* (MO, PMA). DARIÉN: Just S of El Real, wooded ridge, *Duke 5043* (MO). Quebrada Nigua below Santa Fé, *Duke 8829* (MO). Río Chucunaque above confluence with Río Tuquesa, near Campamento Buena Vista, *Stern et al. 915* (GH, MO, US). 3 mi. N of Santa Fé, *Tyson et al. 4624* (MO). Río Sabana, *No. 117*, collector unknown, ex herb. Roi Leopold II (MO). LOS SANTOS: 11 mi. N of Tonosí, *Tyson et al. 2978* (MO). PANAMÁ: Río Bayano near crossing of Pan American Highway, above confluence with Río Chepo, *Duke 3996* (MO). Río Mamoní 4 mi. beyond Chepo on Pan American Highway, *Duke 5569* (MO). Between Cañasas and Sabalo, 100 m, *Duke 14451* (MO, WIS). Pacora, *Dwyer 1224* (MO).

26. **Solanum rugosum** Dun. *in* DC., Prodr., 13(1): 108. 1852. LECTOTYPE: Brazil, *Blanchet s.n.* (P).

Shrub or *tree* to 5 m tall; twigs often drying blackish, densely pubescent with sessile, porrect, pauciradiate, mostly sessile stellae. *Leaves* to 7 cm wide and 25 cm long, broadly lanceolate, margins sometimes slightly revolute, acuminate apically and basally, above scabrous with dispersed, sessile, porrect, pauciradiate stellae, beneath with somewhat larger but similar hairs; minor leaves wanting. *Inflorescence* a long-stalked, many-flowered cyme standing well above the foliage, the peduncle to 20 cm long, branching in the upper portion, puberulent to tomentose with sessile, porrect stellae, pedicels 2–9 mm long, slender, pubescent, abscissing almost at the base. *Flowers* with the calyx 3–5 mm long, lobed to halfway down, the lobes deltoid, a glabrate region at the base of the calyx often drying dark or appearing swollen but not forming a large and conspicuous annular enlargement; corolla white, drying yellowish-brown, 15 mm across, lobed to more than halfway down; anthers 3 mm long, the filaments glabrous; ovary glabrous or pubescent. *Fruits* yellow, glabrescent, 9–11 mm across; seeds 2 mm long.

Solanum rugosum is similar to *S. asperum* but differs in having broader leaves which are more pubescent above and have sessile stellate hairs beneath. The dark area at the base of the calyx is useful in recognition of dried specimens.

This species occurs at roadsides and in forest openings in lowland and middle elevation areas in Panama. The species ranges from British Honduras to Brazil and is present in both Greater and Lesser Antilles.

BOCAS DEL TORO: Between El Hato de Volcán and Costa Rica, along road, lumbered over area, 5,000–6,000 ft, *Ebinger 818* (MO). Junction of Changuinola and Tuibe rivers out Zigla road, along wet bank of river, *Lazor et al. 2553* (FSU, SCZ). Almirante near road to Chiriquí, *McDaniel 5076* (FSU, MO). Water Valley, *von Wedel 972* (GH, MO, US). Fish Creek Hills, vicinity of Chiriquí Lagoon, *von Wedel 2424* (GH, MO, US). Isla Colón, *von Wedel 2844* (MO). CANAL ZONE: Barro Colorado Island, *Aviles 64* (MO). Vicinity of Hill

C-6, Ft. Sherman, *Duke 4356* (MO). Gamboa naval reservation, second growth forest, *Ebinger 905* (MO, US). Barro Colorado Island, *Miller 22* (MO, US); *Shattuck 475* (MO, US). COCLÉ: N rim of El Valle, *Allen 1851* (GH, MO, US). 2 mi. above El Valle on road to La Mesa, *Croat 13308* (MO). Cerro Pilón, hill below summit, above El Valle de Antón, 2,000–2,700 ft, rain forest, *Dwyer et al. 4523* (MO). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7942* (MO). COLÓN: Santa Rita, selva alta perennifolia, secundaria, *Gómez-Pompa et al. 3207* (MO). On road to Piña, *Kirkbride & Hayden 328* (MO, NY). Salud, "Muñeco," *Lao & Holdridge 217* (MO). DARIÉN: Caña and vicinity, 2,000–6,500 ft, *Williams 826* (NY). PANAMÁ: 10 mi. S of Goofy Lake on road to Cerro Jefe, *Correa & Dressler 156* (MO). 3 mi. above Goofy Lake near Cerro Azul, *Croat 11574* (SCZ). 2 mi. beyond Goofy Lake on road to Cerro Azul, *Croat 13019* (MO, right hand specimen only). Cerro Campana, 3,000 ft, above Su Lin Motel, dense woodland bordering roadside, *Dwyer & Kirkbride 7831* (DUKE, MO, NY). La Campana, Cerro Campana, wooded area along road, *Ebinger 334* (MO). Summit of Cerro Jefe and forests along road beyond summit, *Hayden 1023* (MO). Cerro Azul, roadside woods and thickets, *Porter et al. 4082* (MO). Cerro Azul, *Rodriguez 2* (DUKE, MO). Cerro Jefe in "*Clusia*" forest, 2,700–3,000 ft, *Tyson et al. 3317, 3318* (both MO). Cerro Azul, *Wendehake 2* (MO).

27. **Solanum umbellatum** Mill., Gard. Dict., ed. 8. 1768. TYPE: Mexico, *Houston s.n.* (BM).

S. cortex-virens Dun. *in* DC., Prodr. 13(1): 372. 1852. TYPE: Based on *S. umbellatum* Mill.
S. receptum Van Heurck & Müll.-Arg., Obs. Bot. 1: 46. 1881. SYNTYPE: Costa Rica, *Botteri 852* (BM, K).

Shrubs or *trees* 1–3(–7) m tall; twigs loosely pubescent with long-stalked, pauciradiate hairs, the stalks multiseriate and stout. *Leaves* to 20 cm long and 10 cm broad, lanceolate to elliptic, narrowed at each end, above usually drying dark with small, dispersed, sessile, porrect stellae; minor leaves usually ovate to lanceolate, pointed. *Inflorescence* a long-stalked cyme standing well above the foliage, the peduncle branching in the upper portion, loosely pubescent or tomentose with pauciradiate stellae on multiseriate stalks; pedicels 3–6 mm long, pubescent, articulating at the base. *Flowers* with the calyx 2–5 mm long, lobed ¾ the way or more, tomentose or glabrescent, glabrous within; corolla white, drying olivaceous or brownish, 10–15 mm across, tomentose without, lobed slightly to deeply; filaments glabrous, the anthers 3 mm long; ovary glabrate. *Fruits* 8–10 mm across, yellow when ripe, glabrous; seeds 1.5–2 mm long.

This species is distinct in the shaggy pubescence of the inflorescence, which consists in part of porrect stellae on long coarse multiseriate stalks.

Solanum umbellatum is a species of roadsides, second growth woodland, cafetales, pastures, and other woody vegetation which follows disturbance. It occurs at lower elevations and ascends to middle and upper elevations. The species ranges from northern Mexico east at least to Colombia and the Greater Antilles.

BOCAS DEL TORO: Changuinola to 5 mi. S at junction of Río Changuinola and Río Teribe, 100–200 ft, *Lewis et al. 835* (GH, MO, US). CANAL ZONE: Corozal, *Greenman & Greenman 5193* (MO). Without locality, *Hayes s.n.* (BM). Ancón Hill, *Killip 3026* (MO). Curundu, *Tyson 6291* (FSU, MO). Vicinity of Miraflores, *White 118* (MO, US). Barro Colorado Island, *Croat 4068* (MO), *5106* (MO, NY), *6007, 7391* (MO); *Greenman & Greenman 5225* (MO); *Wetmore & Abbe 49* (A, GH, MO). CHIRIQUÍ: Bajo Mono-Robalo Trail, W slopes of Cerro Horqueta, 5,000–7,000 ft, *Allen 4828* (MO). S side of Cerro Pando, shrub in banana patch, 6,000 ft, *D'Arcy 5388* (GH, MO, NY, P). Above Paseo la Canoa, 3,000 ft, *D'Arcy 5429* (ADW, MO). 1 mi. N of La Frontera, *D'Arcy 5436* (MO, MPU). Above Boquete,

4,800 ft, shrub on roadside, *D'Arcy 5439* (MO). Cerro Horqueta, 1,500 m, *Duke et al. 13656* (MO). Without locality, *Hayden 168* (MO). Tolé, *Tyson et al. 4221* (FSU, MO). Finca Lérida to Boquete, 1,300–1,700 m, *Woodson et al. 1145* (A, MO, NA, NY). Río Chiriquí to Remedios, 15–50 m, *Woodson et al. 1184* (A, MO). COCLÉ: Mountains above El Valle, *Stimson 5001* (NY). COLÓN: Nueva Chagres, beach and adjacent roadside, *Lewis et al. 1855* (GH, MO). HERRERA: Between El Potrero and Las Minas, *D'Arcy & Croat 4136* (MO). Road between Las Minas and Pesé, *Duke 12309* (MO, WIS), *12341* (MO). LOS SANTOS: 17.8 mi. S of Macaracas, 1,100 ft, roadside and secondary woods, *Lewis et al. 1613* (GH, MO, US). PANAMÁ: 3 mi. above Goofy Lake near Cerro Azul, *Croat 11573* (MO). Río Cañita, open grazed area near Jenine along Pan American Highway, *Duke 3810* (GH, MO), *3814* (MO). Río Pacora just below confluence with Río Corso, *Duke 12006* (MO, WIS). Camp Tiotuma, helipad in premontane rain forest, *Duke 15507* (WIS). Tocumen, *Dwyer 1846A* (GH, MO, US), *1851* (MO). Altos del Río Pacora, 2,500 ft, edge of river and cloud forest, *Lewis et al. 2311* (MO). Cañita, 18 mi. E of Chepo, *Tyson & Smith 4140* (MO). Cerro Jefe, *Tyson et al. 4306* (FSU, MO). Isla Taboga, *Woodson et al. 1458* (A, MO, NA, NY). VERAGUAS: Between Tolé and Santiago, 50 mi. from Santiago, down embankment to river edge, *Kirkbride & Hayden 170* (MO).

J. Section **Extensum** D'Arcy, Ann. Missouri Bot. Gard. 59: 268. 1972 [1973]. TYPE: S. *extensum* Bitt.

Trees or scandent *shrubs*, unarmed, pubescence of porrect stellae. *Leaves* simple and entire, ovate or elliptic; petiolate; minor leaves present, often at dichotomies of the stem. *Inflorescence* lateral or opposite the leaves, sometimes almost terminal, a congested short panicle or raceme, subumbellate or appearing fascicled on the stem; pedicels slender, deciduous at the base. *Flowers* small; calyx lobed to various degrees, sometimes unequally so, sometimes subfoliaceous and accrescent in fruit; corolla white, deeply lobed; anthers equal, short, stout, opening introrsely by large terminal pores; ovary glabrous or pubescent. *Fruit* a globose, juicy berry, glabrous or pubescent; seeds compressed.

Species in this section have stellate hairs and small flowers with small stout anthers opening by large terminal pores. They show great uniformity of leaf shape and overall appearance. There are perhaps a dozen species of Central and South America. *Solanum schlechtendalianum* may be the only species present in the Antilles. An unusual aspect of the Panamanian species is that they bloom and fruit in the fourth quarter of the year, a time of heavy rains when blooming is reducted in most species of Solanaceae.

a. Leaves whitish or light tomentose beneath, glabrate and drying dark green above, the two sides strongly contrasting; fruit pubescent ..... 31. S. *schlechtendalianum*
aa. Leaf sides not strongly contrasting; fruit glabrous.
  b. Young parts villous; leaf uppersides with dense stellae.
    c. Leaves ovate, none narrowly lanceolate ..... 29. S. *extensum*
    cc. Many leaves narrowly lanceolate ..... 30. S. *perattenuatum*
  bb. Young parts appressed-pubescent; leaf uppersides with dispersed stellae ..... 28. S. *cordavense*

28. **Solanum cordavense** Sessé & Moc., Fl. Mex., ed. 2. 51. 1894. TYPE: (not seen).

S. *lundellii* Standl., Publ. Field Columbian Mus., Bot. ser. 8: 42. 1930. TYPE: British Honduras, *Lundell 324* (F).
S. *edwardsii* Standl., Trop. Woods 37: 31. 1934. TYPE: Honduras, *Edwards 639* (GH, NY, US).

Shrub or *tree*, sometimes scandent to 5 m tall; twigs slender, tomentose with stalked and sessile porrect hairs, glabrescent. *Leaves* to 15 cm long and 5 cm broad, ovate or elliptic, slightly oblique, acuminate apically, rounded or obtuse basally, sometimes dimidiate, above dispersed pubescent with sessile, porrect hairs, their midpoints long, beneath dispersed to densely pubescent with sessile and stalked multangulate hairs; petiole short, to 6 mm long; some minor leaves present. *Inflorescence* lateral, a few- to several-flowered, stalked or almost sessile subumbellate raceme, the peduncle stout, to 2 cm long, tomentose; pedicels to 2 cm long, tomentose with stalked and sessile multangulate stellae, the radii contributing to the pubescence as much or more than the midpoints, some hairs perhaps dendritic rather than truly stellate. *Flowers* small, calyx 3 cm long, lobed halfway, the lobes obtuse, becoming much larger and subfoliaceous in fruit, to 6 mm long and 3 mm broad; corolla white, 15 mm across, reflexed, drying orange with a prominent dark midvein, lobed ¾ the way down, the lobes obtuse; filaments glabrous, connate basally, the anthers stout 2–3 mm long; style glabrous, exserted 2–3 mm. *Fruit* a white berry 8–10 mm across.

On the herbarium sheet, this species is superficially indistinguishable from specimens of S. *extensum* without well developed tomentum. Smaller midpoints on the stellae and a difference in the appearance of the two sides of the leaves are good distinctions. Judging from collectors' notes, the two species also differ in fruit color and habit.

CHIRIQUÍ: Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, premontane rain forest (oak), *Kirkbride & Duke 906* (MO). Salta-Camiseta Trail, Volcán de Chiriquí, Boquete District, 5,000 ft, *Terry 1362* (MO). Río Chiriquí Viejo Valley, *White 60* (MO, US). Río Chiriquí Viejo Valley near Rivera's coffee finca, *White 165* (GH, MO, US).

29. **Solanum extensum** Bitt., Fedde Repert. 13: 94–95. 1913. LECTOTYPE: Panama, *Williams 704* (US; NY, isolectotype). PARATYPE: Colombia, *Sonntag 8* (P).—FIG. 23.

Clambering *shrub* to 7 m long; twigs slender, viscid-pilose with mostly sessile porrect stellae bearing very long midpoints, these often gland-tipped. *Leaves* to 15 cm long and 7 cm broad, ovate, slightly oblique, apically acuminate, basally rounded or obtuse, above pilose to viscid-tomentose with sessile, porrect stellae bearing long midpoints, beneath much the same color with mostly sessile, but a few long-stalked, multangulate or porrect hairs; petioles to 7 cm long. *Inflorescence* terminal or becoming lateral, a few- to several-flowered fascicle or subumbellate on a short, pilose peduncle; pedicels to 3 cm long but often very short, slender, villous with very short-radiate stellae bearing long (to 3 mm) glandular midpoints. *Flowers* small, calyx green, subfoliaceous, deeply lobed, the lobes oblong, unequal, accrescent to 10 mm long in fruit, pubescent outside and about halfway down inside; corolla white, drying with a prominent midvein, ca. 10 mm across, deeply lobed, the lobes somewhat unequal; anthers stout, ca. 3 mm long, opening by large, introrse apical pores and also lengthwise; ovary and the style glabrous. *Fruit* a globose, black berry, 5–8 mm across; seeds compressed-discoid, 3 mm across.

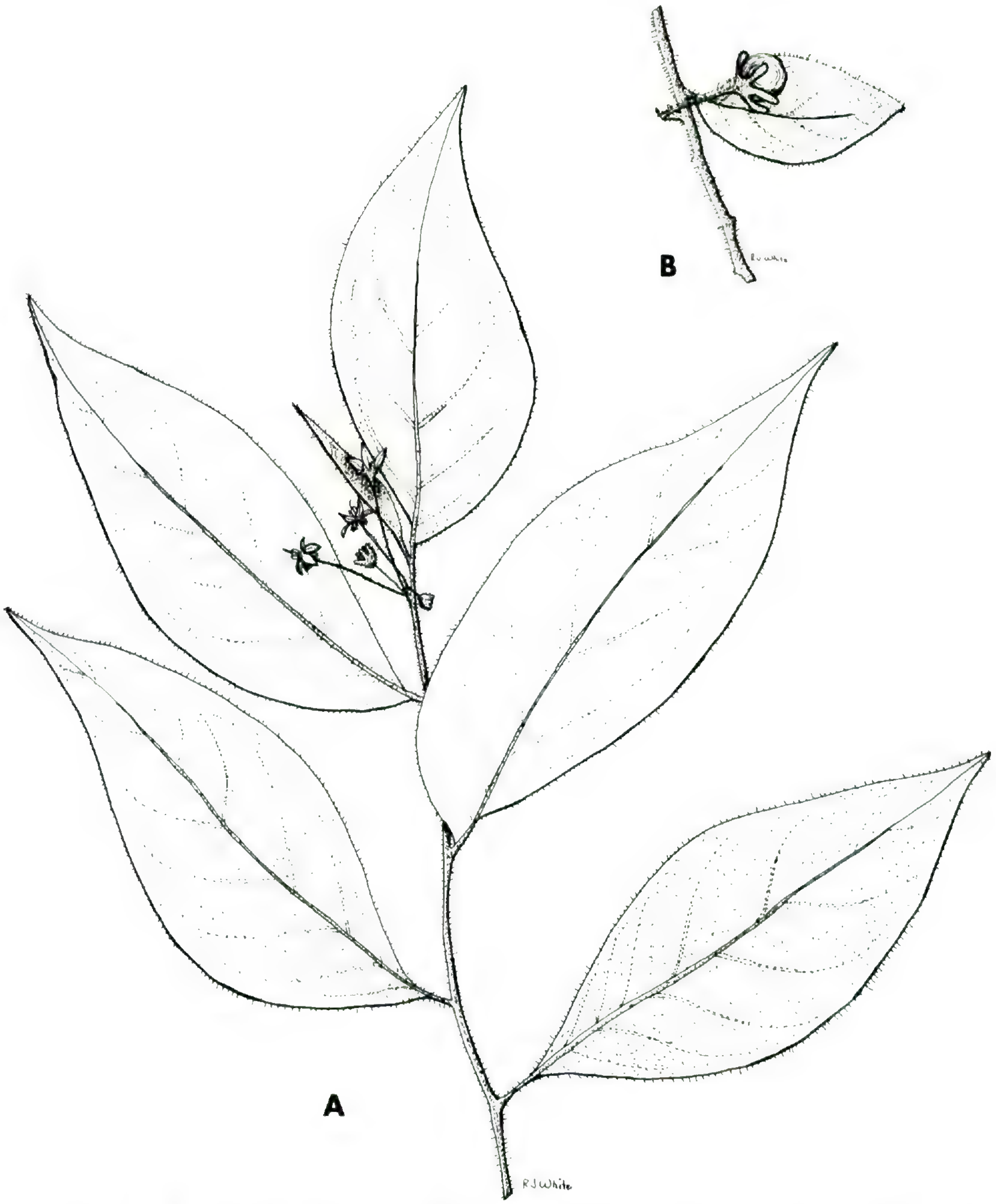

Figure 23. *Solanum extensum* Bitt.—A. Flowering branch (× ½). [After *Tyson 1842* (SCZ).]—B. Fruit (× ½). [After *Stern et al.* 332 (MO).]

Solanum extensum has a number of very close relatives with which it is often confused. *Solanum umbratile* J. R. Johnst., of Venezuela (Isla Margarita), has smaller flowers and seemingly stiff, eglandular midpoints on the hairs of the pedicel. It also has smaller leaves. *Solanum cordavense* Sessé & Moc. has white fruits, and the radii and midpoints of the stellae are more nearly equal in length, the radii having an important role in the pubescent appearance of the pedicels. *Solanum perattenuatum* I. M. Johnst. may in fact be specifically synonymous with

S. extensum but looks quite different. *Solanum didymum* Dun. of South America has finer pubescence and the midpoints are mostly two-celled.

CANAL ZONE: Fort Clayton near old hospital building, *Dwyer 3924* (MO). Farfan Beach, *Dwyer 6775* (MO). Chagres, *Fendler 252* (MO). Pan American Highway toward Nuevo Emperador, *Lewis et al. 5228* (F, MO, PMA). Near Old Fort Lorenzo, mouth of Río Chagres, *Piper 5906, 5920, 5942* (all US). Near Río Cocolí, along roadside, *Stern 332* (GH, MO, US). Howard Air Force Base, *Tyson 1842* (FSU, MO, SCZ). PANAMÁ: Cermeño, *Dwyer & Robyns 107* (MO). San José Island, Río Marino below Red Hill, *Johnston 101* (GH, MO, US). San José Island, air strip, *Johnston 537* (GH, US). San José Island, Dead End Road, common, half scrambling in thickets, *Johnston 1035* (GH, MO, US). Sabanas N of Panama City, *Paul 458* (US). Río Tapía, moist thicket, *Standley 26207* (US). Río Tocumen, wet forest, *Standley 26741, 29337* (both US).

30. **Solanum perattenuatum** I. M. Johnst., Sargentia 8: 265. 1949. TYPE: Panama, *Johnston 909* (GH, MO).

Slender, much branched *shrub* to 1.8 m tall; twigs tomentose with sessile, porrect stellae bearing much reduced radii and long, gland-tipped midpoints. *Leaves* to 8 cm long, lanceolate to elliptical or ovate, apically long acuminate or acuminate, basally narrowed, above hirsute with hairs like those of the twigs, beneath with sessile and stalked, multangulate hairs; petioles lax, to 12 mm long. *Inflorescence* several- to many-flowered, terminal, often becoming lateral, a sub-umbellate raceme; the peduncle short, 3 mm long or less. *Flowers* small, calyx 3–4 mm long, deeply lobed, the lobes green, villous; corolla drying testaceous, 8–11 mm across; anthers stout, less than 2 mm long; style glabrous, exserted ca. 2 mm. *Fruit* unknown.

"The leaves are distinctive. They tend to hang downward from the twigs and are 5–10 cm long, and though rarely as much as 45 mm broad, are usually only 1–10 mm in width." They usually have "a whip-like apical attenuation" (Johnston). The flowers are slightly smaller than those of *S. extensum*. Johnston speculated, and the appearance of the type collection bears him out, that the appearance of this taxon might be due to a virus acting on *S. extensum*.

It is known only from the Perlas Archipelago, two collections taken by Johnston.

PANAMÁ: San José Island, main camp, second growth near the Guard House, *Johnston 909* (GH, MO), *1034* (GH, US).

31. **Solanum schlechtendalianum** Walp., Repert. Bot. Syst. 3: 61. 1844. TYPE: Based on *S. geminifolium* Schlecht.

S. geminifolium Schlecht., Linnaea 5: 112. 1830, err. typogr. *S. geminiflorum* corrected Linnaea 8: 255. 1833, nom Thonn. *in* Schum. & Thonn., Beskr. Guin. Pl. 121. 1827. TYPE: *Schiede 138* (MO[38]).

S. fragile Wright *ex* Griseb., Cat. Pl. Cub. 189. 1866. TYPE: Cuba, *Wright 3024* (GH, MO, P).

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[38] This specimen is from the Bernhardi Herbarium. *Schiede 138* and *Schiede 137*, type of *S. hygrophilum* Schlecht., are transposed on their respective herbarium sheets, each specimen bearing the label information of the other. A photograph (MO) of *Schiede 137* from Geneva (G-DC) is a good match for the Missouri specimen labelled *Schiede 138*, while the Missouri specimen labelled as *Schiede 137* agrees with the description of *S. geminifolium* Schlecht.

S. *gentlei* Lundell, Publ. Field Columbian Mus., Bot. ser. 8: 42. 1930. TYPE: British Honduras, *Gentle 3944* (A, NY).

Shrub or *tree* to 8 m tall; twigs finely tomentose with whitish, appressed, stalked, porrect stellae, soon glabrescent leaving a powdery surface. *Leaves* to 15 cm long, ovate, apically acuminate, basally rounded, above green, sometimes drying dark, with fine, sessile, porrect, pauciradiate hairs, beneath hoary with appressed, stalked stellae; petiole short, to 8 mm long; minor leaves often present, often associated with dichotomies of the stem rather than solitary major leaves. *Inflorescence* almost terminal or becoming opposite the leaves or occasionally lateral, an open panicle, the peduncle unbranched or ternately branched, densely pubescent; pedicels 3–6 mm long becoming 10–15 mm long but not stout in fruit. *Flowers* small; calyx 3 mm long, lobed ⅓–½ the way down, the lobes short-deltoid, the midvein evident, 1.5 mm long in flower, becoming 3 mm long in fruit, densely pubescent outside, glabrous within; corolla white, 7–9 mm across, deeply lobed, the lobes appressed tomentose outside, glabrous within; filaments glabrous, connate basally, the anthers 2.5–3 mm long, stout, opening introrsely by large terminal pores; ovary persistently tomentose, the style pubescent on the basal half. *Fruit* a globose berry, maturing purple (Lewis), 7–9 mm across; seed flattened-discoid, 2 mm across.

This species occurs in forest openings at lower and middle elevations. It ranges from Mexico and the Antilles south to the Andes.

Solanum schlechtendalianum is placed in sect. *Extensum* for convenience; it may not be closely related to other members of the section.

BOCAS DEL TORO: Quebrada Huron, rapid streams through evergreen seasonal forest, *Kirkbride & Duke 431* (MO, NY). 4–6 mi. N of Almirante, lower montane rain-forest, *McDaniel 5100* (FSU, MO). CANAL ZONE: Madden Forest Preserve along Las Cruces Trail and highway, deep rain forest, *Lewis et al. 5262, 5307* (both MO). COLÓN: Santa Rita East Ridge, *Dwyer 8415* (MO). Between France Field and Catival, *Standley 30374* (US). DARIÉN: Cana and vicinity, *Williams 729* (NY). HERRERA: 12.5 mi. S of Ocú, 1,200 ft, secondary woods on hillside, *Lewis et al. 1649* (GH, MO, US). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11832* (MO, NY, OS), *11868* (MO, OS). Loma Prieta, Cerro Grande, 2,400–2,800 ft, cloud forest and disturbed margins, *Lewis et al. 2200* (DUKE, MO). PANAMÁ: Roadside, Cerro Jefe, *D'Arcy et al. 3962* (MO). Cerro Jefe near Río Indio, 2,100–2,200 ft, *Duke 15239* (WIS). 1 mi. N of Cerro Azul, 2,300 ft, *Tyson & Blum 4075* (FSU, MO).

K. Section **Holophylla** (Don) Walp., Repert. Bot. Syst. 3: 51–57. 1844.

Subsect. *Holophylla* G. Don, Gen. Syst. 4: 414–418. 1838. LECTOTYPE: *S. pubigerum* Dun.

Unarmed *shrubs* or *trees*; twigs with dendritic or subechinoid hairs. *Leaves* entire, the margins often revolute, the pubescence on the undersides evenly distributed or concentrated in the vein axils; minor leaves sometimes present. *Inflorescence* mostly terminal, sometimes becoming lateral, axillary or opposite the leaves, an upright panicle or corymb or subumbellate at the ends of short peduncles. *Flowers* with the calyx small; corolla white or purple, deeply lobed; anthers opening by large, introrse, terminal pores; ovary glabrate. *Fruit* globose, not large, glabrous; seeds compressed.

Species of this section range from northern Mexico to Argentina. Perhaps not

a natural group, plants in this section are easily recognized by the dendritic or echinoid hairs.

a. Liana; inflorescence pendulous, more than 10 cm long ..... 32. *S. ipomoea*
aa. Shrub or tree; inflorescence erect, nodding or horizontal, not pendulous, less than 8 cm long.
  b. Inflorescence an upright, open panicle 5–8 cm long; flowering pedicels with conspicuous, expanded articulation points ..... 34. *S. storkii*
  bb. Inflorescence congested and appearing umbellate, less than 4 cm long; flowering pedicels without noticeable articulation points.
    c. Leaves copiously pubescent beneath ..... 33b. *S. microleprodes* var. *felices*
    cc. Leaves puberulent to glabrate beneath .. 33a. *S. microleprodes* var. *microleprodes*

32. **Solanum ipomoea** Sendt. *in* Mart., Fl. Bras. 10: 50–51. 1846. TYPE: Brazil, *Martius s.n.* (M, not seen; MO, photo).

Liana festooning in shrubs; twigs slender, flexuous, velutinous with dendritic hairs but glabrescent. *Leaves* to 10 cm long, cordate, the margins slightly revolute, above with scattered simple and dendritic hairs, beneath velutinous with copious, erect, dendritic hairs; petiole 1.5–3 cm long, pubescent on the distal portion; minor leaves wanting on material seen but tomentose axillary buds present. *Inflorescence* terminal, perhaps becoming opposite the leaves or axillary, a pendant, several- to many-flowered open panicle to 60 cm long, the peduncle velutinous with internodes 1–4 cm long, the basal portion with foliose bracts gradually reduced in size to about ⅔ the length, the racemes long-stalked (5–25 mm), the cincinnus terminal and congested; pedicels slender, 4 mm long, tomentose on the lower half, obconical above, articulating at the base. *Flowers* with the calyx drying russet-brown, 3 cm long, glabrate, lobed ⅓ the way down, the lobes obtuse; corolla ?pink, lobed nearly to the base, the lobes 6–7 mm long, lanceolate, thick, farinose outside and with occasional dendritic hairs; anthers opening by large terminal pores. *Fruit* not seen.

This species is distinctive among members of the genus *Solanum* in Panama in its unarmed lianous habit, soft, erect, dendritic hairs and cordate leaves. It superficially resembles some South American species of *Cyphomandra*, *e.g. C. reitzii* Smith & Downs and *C. angustifolia* Smith & Downs, both of Brazil.

CANAL ZONE: Agua Clara on the Trinidad River, 10–40 m, climbing on bushes in inundated places, long racemes hanging, *Pittier 3996* (US).

33. **Solanum microleprodes** Bitt., Fedde Repert. 13: 96. 1913. HOLOTYPE: Panama, Boca de Pauarandó, at Río Sambu, Darién, *Pittier 5686* (US-715968; US, isotypes).

33a. **Solanum microleprodes** Bitt. var. **microleprodes.**

Shrub or *tree* to 4 m tall; twigs scurfy-tomentose with dendritic-echinoid hairs. *Leaves* to 25 cm long, elliptic or broadly elliptic, apically acuminate, basally obtuse, glabrate above with scattered simple and dendritic hairs, beneath sparingly pubescent with mostly dendritic hairs; petiole ca. 2 cm long; rotund minor leaves often present. *Inflorescence* opposite the leaves or lateral, several-flowered, subumbellate; the peduncle short, to 25 mm long, usually once-branched at the

apex; pedicels 1 cm long, tomentose, becoming stout but not much longer in fruit. *Flowers* small, calyx 2 mm long, tomentose, short-lobed, somewhat larger in fruit; corolla white, 12–15 mm across, lobed nearly to the base, anthers (Bitter) ca. 4 mm long, ellipsoid, opening by oblique apical pores; ovary with small, spreading, simple or dendritic hairs. *Fruit* globose, 15–20 mm across; seeds much compressed, 3 mm across.

Superficially this species resembles S. *brenesii* Mort. & Standl. (sect. *Leiodendra*), of Costa Rica, but that species is mostly glabrous and its calyx is glabrate. *Solanum microleprodes* is closely related to S. *chlamydogynum* Bitt. (Lectotype: Venezuela, *Pittier 5862* (US)), which has copiously pubescent leaf undersides and larger and more pubescent inflorescences and flowers.

Most collections are from Darién, but Pittier collected it in the Chiriquí lowlands, and Allen collected it in Veraguas Province.

CHIRIQUÍ: Remedios and vicinity, 0–100 m, *Pittier 5465* (US). DARIÉN: Road from El Real to Pinogana, *Duke 5152* (MO). Río Balsa between Río Arenti and Manene, *Duke 8791* (MO, OS). Agua Fria, 8 mi. N of Santa Fé, 50 m, *Duke 10109* (MO, US, WIS). Vicinity of Paya, Río Paya, along trail from Paya to Pucro, *Stern et al. 239* (GH, MO, US). On trail from Paya to Pucro, wet forested area, *Stern et al. 417* (GH, MO, US). 3 mi. N of Santa Fé, *Tyson et al. 4636* (FSU, MO, SCZ). VERAGUAS: Headwaters of Río Cañazas, trail between Cañazas and the foot of the Cordillera Central, 300–600 m, *Allen 202* (MO).

33b. **Solanum microleprodes** var. **felicis** D'Arcy.[39] HOLOTYPE: Panama, *Pittier 5173* (US).

This variety differs from var. *microleprodes* in the leaf undersides being softly pubescent with copious, erect, dendritic hairs and almost without sessile, subechinoid hairs.

Variety *felicis* is known only from the type collection.

CHIRIQUÍ: Vicinity of San Felix, 0–120 m, *Pittier 5173* (US).

34. **Solanum storkii** Mort. & Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1093. 1938. TYPE: Costa Rica, *Stork 3023* (F).

Shrub or *tree* to 3 m tall; twigs finely tomentose and appearing granular, with sessile or erect, subechinoid or dendritic hairs, glabrescent. *Leaves* to 15 cm long, lanceolate, narrowed at base and apex, mostly widest at or below the middle, margins slightly revolute, pubescent above and beneath with sparse, minute, sessile, echinoid hairs, mostly drying dark above; petioles 5–10 mm long grading into the leaf base; minor leaves sometimes present, mostly caducous. *Inflorescence* terminal, often lateral or opposite the leaves in fruit, an erect panicle 5–8 cm long, the peduncle glabrescent, branching 2 or 3 times from a central axis, elongating in fruit; pedicels filiform, 10 mm long, dispersed pubescent with a conspicuous, discoid swelling on the peduncle at its basal articulation. *Calyx* 3–5 mm long, broadly cupuliform, subtruncate with small narrow teeth which enlarge as the sinuses split during corolla egress, sparingly pulverulentous outside; corolla purple, farinaceous outside, ca. 15 mm across, deeply lobed;

[39] *Solanum microleprodes* var. *felicis* D'Arcy, var. nov. Varietas differt a var. typice foliis subter pilis dendriticis erectis copiosis tectis fere sine pilis sessilibus subechinoideis.

filaments glabrous, the anthers elongoid or tapering slightly, 5 mm long, opening by large terminal pores which dry with conspicuous yellow rims; ovary and the style glabrous. *Fruit* globose, 6–8 mm across, purplish black (*Holm & Iltis 142* (MO), Costa Rica).

This species is distinctive in its inflorescence, reminiscent of sect. *Leiodendra*, and in its granular puberulence of echinoid hairs. The glabrous ovary is unlike that of Panamanian species of sect. *Leiodendron*. The enlarged pedicel articulation points are a good feature for recognition.

Solanum storkii is much like South American plants going under the names *S. pubigerum* Dun. (= ?*S. cervantesii* Lag., ?*S. pulverentulum* Pers., non Lam.). Study of a range of Peruvian material will be necessary to establish the differences.

CHIRIQUÍ: Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 4* (MO).

Subgenus **Bassovia** (Aubl.) Bitt., Fedde Repert. 17: 329–330. 1921.

Bassovia Aubl., Hist. Pl. Guiane Fr. 1: 217; 3: *tab.* 85. 1775. TYPE: *B. sylvatica* Aubl. (= *Solanum* sp.).

Herbs, *shrubs* or *trees*, some root climbers, some procumbent, glabrous or variously pubescent with short, multicelled, uniseriate hairs. *Leaves* simple or pinnate, the leaflets subentire; petioles clasping at the base. *Inflorescence* axillary or lateral and opposite an adventitious root, sometimes paired, a several-flowered raceme, the peduncle sometimes branched with a conspicuous cicatrix of pedicel scars. *Flowers* small; calyces hardly accrescent; corollas deeply lobed; anthers stout, dehiscent by large introrse, terminal pores and by prominent lateral slits. *Fruits* globose to turbinate-conical, usually conspicuously apiculate, sometimes laterally flattened; seeds not flattened.

This group includes plants which bear their inflorescences in a position characterized as axillary, although the inflorescence may stand at a dichotomy of the stem, and in section *Herpystichum*, it has been moved through concaulescence to a position lateral on the stem. For a discussion of concaulescence and the variants to this branching pattern, see Danert (Bereich. Abh. Deutsch. Akad. Wiss. Berlin 6. 1958). One feature of the branching pattern in subgenus *Bassovia* is that the petiole bases are usually somewhat clasping. The clasping petiole base and inflorescence standing at the stem dichotomy are usual in the genus *Cyphomandra* and in section *Archaesolanum*, a small group of *Solanum* species from New Zealand-Australian region. There is an overall similarity between plants of subgenus *Archaesolanum* and section *Bassovia* and between the anthers of subgenus *Archaesolanum* and those of section *Herpystichum*.

Plants of this subgenus occur mostly in deep forests from Mexico to Peru.

L. Section **Herpystichum** Bitt., Fedde Repert. 17: 33. 1921. TYPE: *S. trifolium* Dun.

Procumbent creeping *herbs*, glabrate to pilose with simple hairs. *Leaves* 3–5-odd-pinnate, solitary at the nodes, the long petiole clasping the stem; minor

leaves minute, simple, axillary when present. *Inflorescence* lateral, ebracteate but placed opposite an adventitious root, occurring about every fifth or sixth leaf, a few-flowered, open raceme on an elongate slender peduncle which is slightly clasping at the base. *Flowers* small, calyx short-lobed; corolla deeply parted; stamens equal, the filaments glabrous, the anthers short and stout, dehiscing by large introrse apical pores and also by longitudinal slits; ovary glabrous. *Fruit* a berry, globose, rhombic or obturbinate and flattened, short-stipitate or sessile in the calyx.

A small group of seldom-collected plants ranging from Peru to Mexico. They are very striking in habit and overall appearance. The clasping petiole and peduncle base and the shape of the fruit of *S. phaseoloides* argue for placement in subgenus *Bassovia*. The inflorescences are lateral, appearing on the side of the stem as the preceding leaf, actually an ancestrally axillary inflorescence carried for some distance up the stem, taking with it a part of the meristem producing an adventitious root.

35. **Solanum phaseoloides** Polak., Linnaea 41: 585. 1877. TYPE: (not seen).

S. olivaeforme Donn. Sm., Bot. Gaz. (Crawfordsville) 14: 28–29. 1899. TYPE: Guatemala, *Türckheim 1226* (K, US).

Procumbent, apparently succulent *herb* to 10 m long, glabrate. *Leaves* trifoliolate, the leaflets with conspicuous (to 5 mm long) petiolules, suborbicular to rhomboid, apically obtuse, basally rounded, to 4 cm long, the lateral pair smaller and often oblique at the base; petioles slender and elongate, to 5 cm long, slightly clasping the stem. *Inflorescence* axillary or lateral, an open, few-flowered raceme, the peduncle to 6 cm long, very slender; pedicels ca. 2 cm long. *Flowers* with the calyx short-campanulate with 5 rotund lobes; corolla white, ca. 1 cm across, lobed nearly to the base; stamens equal, the filaments united basally, ca. 1 mm long and continuing in a relatively broad connective, the anthers stout, 1.5–2.5 mm long; ovary conical, the style clavate in the upper portion, the stigma globose. *Fruit* "flattened like a lance" (*Jiménez 1222* (US), Costa Rica), the outline obturbinate or rhombic, drying dark, very thin and flat on herbarium sheets, 2–3 cm long.

The trifoliolate leaves, procumbent habit and long, solitary petioles and pedicels are striking characters. The fruit is also distinctive.

Solanum phaseoloides ranges from Panama to Guatemala. Collections seen (mostly from Costa Rica) are from middle to upper elevations. It grows on the floor of wet forests and sometimes hangs from cliffs.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White 82* (MO).

M. Section **Pteroidea** Dun., Hist. Sol. 117, 136–138. 1813. LECTOTYPE: *S. mite* R. & P.

Herbs, *shrubs* or *trees*, some root climbers, glabrous or pubescent with short, multicelled uniseriate hairs. *Leaves* simple or pinnate, the leaflets subentire; minor leaves mostly wanting. *Inflorescence* axillary or at a dichotomy of the stem,

one or a pair of mostly unbranched, several-flowered racemes bearing a conspicuous cicatrix of pedicel scars on the terminal portion. *Flowers* small, calyces hardly accrescent; corollas deeply-lobed; anthers equal, stout, much shorter than the corolla lobes, dehiscent by large introrse terminal pores and by prominent lateral slits. *Fruits* globose to turbinate-conical, sometimes laterally flattened, usually apiculate; seeds not flattened.

A group of perhaps a dozen species of deep moist forests of Central and South America. While the type species of this section and of section *Herpystichum* are very different in appearance, there exist several species which may be considered intermediate. *Solanum diffusum* R. & P. and *S. ternatum* R. & P., both of Peru, are examples of such intermediates, the latter trifoliolate and differing mainly from section *Herpystichum* in the inflorescences being subtended by foliage leaves.

a. Leaves compound, pinnate ..... 37. *S. trizygum*
aa. Leaves simple ..... 36. *S. anceps*

36. **Solanum anceps** R. & P., Fl. Peru 2: 36, *tab. 169*. 1794. TYPE: Peru, collector unknown (MA, not seen; MO, photo).

S. *conjugens* Bitt., Fedde Repert. 11: 12. 1912. TYPE: Ecuador, *Sodiro 114/61* (?B, not seen; MO, photo).
S. *theobromophyllum* Bitt., Fedde Repert. 11: 472. 1912. TYPE: Brazil, *Ule 5490* (W, not seen; MO, photo).

Herb 1–2 m tall, pubescent or glabrous; stems fistulose. *Leaves* simple, entire, 10–30 cm long and 7–16 cm wide, ovate or elliptic, apically long-acuminate, basally obtuse, the lateral veins evident, arcuate; petioles 2–4 cm long. *Inflorescence* axillary, at first terminal and erect, sometimes apically branched and subumbellate, several-flowered, the peduncle puberulent 1–5 cm long, elongating slightly in fruit and bearing congested pedicel scars; pedicels somewhat deflected and 5 mm long in flower, stout, erect and to 10 mm long in fruit. *Flowers* small, calyx 1–2 mm long, glabrous, lobed halfway down, the lobes rotund-deltoid; corolla white, ca. 15 mm across; stamens equal (or perhaps one somewhat longer), the anthers 3–4 mm long, stout, ovate, apically acute, opening by two tiny closely-placed introrse pores. *Fruits* turbinate, laterally flattened, 2.5–3 cm long, white (Ruiz & Pavon), drying black and appearing tuberculate by contraction of the pericarp around the seeds.

This species is distinctive in its axillary inflorescence, large entire leaves and flattened, turbinate fruits. It is a species of deep forests.

COCLÉ: Near El Valle, 800–1000 m, *Allen 1816* (MO). DARIÉN: Boca de Pauarandó on Sambú River, *Pittier 5585* (US). SAN BLAS: Forest SE of Puerto Obaldía, *Croat 16769* (MO).

37. **Solanum trizygum** Bitt., Fedde Repert. 11: 470–471. 1912. TYPE: Venezuela, *Moritz 1644* (?B, not seen; MO, photo).—FIG. 24.

S. *chamaepolybotryon* Bitt., Fedde Repert. 11: 471. 1912. TYPE: Peru, *Spruce 4432* (K, not seen; MO, photo).
S. *fraxinellum* Bitt., Fedde Repert. 11: 469–470. 1912. TYPE: Mexico, *Sartorius s.n.* (W, not seen; MO, photo).

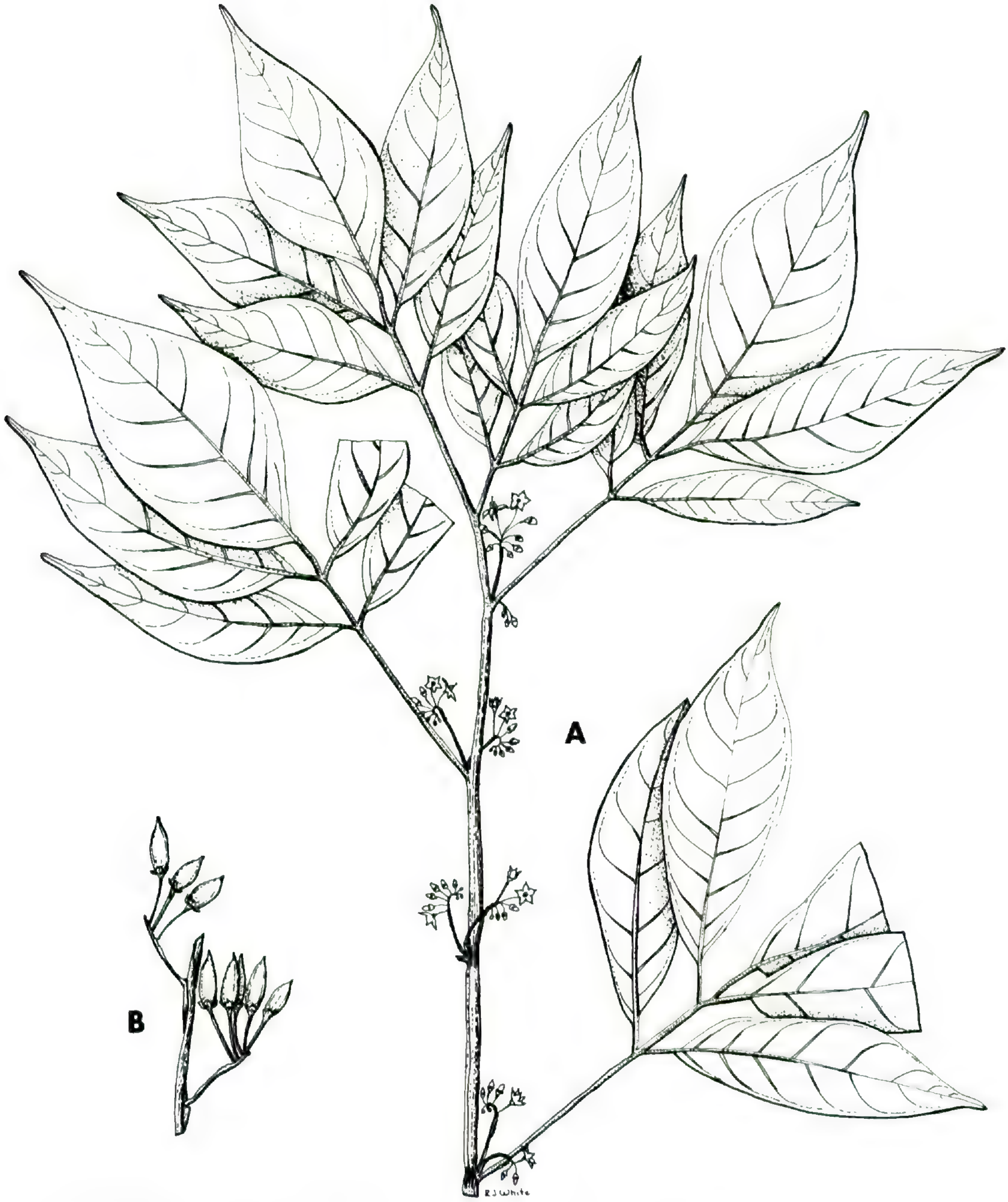

Figure 24. *Solanum trizygum* Bitt.—A. Habit (× ½). [After *Allen 4953* (MO).]—B. Fruit; the berries are flattened, almost two dimensional (× ½). [After *Dwyer & Hayden 7661* (MO).]

Erect, glabrate *herb* 1–1.5 m tall; stems glabrous or occasionally short-pilose, fistulose, the nodes darkening and contracting on drying. *Leaves* 5–9 pinnate, leaflets 4–12 cm long and 1.5–4 cm broad, elliptic to lanceolate, apically long acuminate, basally acute to obtuse, slightly oblique; petioles 4–8 cm long, petiolules 10 mm long or wanting. *Inflorescences* axillary, solitary or paired, short, several-flowered racemes, the peduncles 1–1.5 cm long, slender, glabrous or rarely puberulent, not much enlarging in fruit; pedicels 4–8 mm long, filiform.

Flowers with the calyx 1–1.5 mm long, short-lobed, enlarging slightly in fruit; stamens equal, shorter than the corolla, the filaments short, slender, glabrous, the anthers stout, 2–3 mm long; style exceeding the anthers, the stigma punctiform. *Fruit* a white, laterally flattened, turbinate berry, 2.5–3 cm long, drying black and appearing tuberculate by contraction of the pericarp around the seeds; seeds 2 mm long, prismatic.

A wide ranging species, *S. trizygum* occurs from Mexico to Peru. It is a species of deep forests.

BOCAS DEL TORO: Robalo trail, northern slopes of Cerro Horqueta, 6,000–7,000 ft, *Allen 4953* (MO). CHIRIQUÍ: Bajo Chorro, Boquete district, rain forest, 6,000 ft, *Davidson 63* (MO, US). Boquete, Finca Collins, 5,000 ft, dense woodland, *Dwyer & Hayden 7661* (MO). Woods along Griffen's Trail, Horqueta Mountains, 1,700 m, *Killip 3528* (US). Forests around El Boquete, 100–1,300 m, *Pittier 2986* (US).

Subgenus **Solanum.** TYPE: *S. nigrum* L.

Unarmed *herbs*, *shrubs* or *trees*, pubescent with simple hairs or rarely with branching hairs mixed with simple hairs. *Leaves* simple and entire, toothed or lobed. *Inflorescence* lateral or opposite the leaves, sometimes nearly terminal, the peduncles unbranched or sparingly branched; pedicels abscissing at the base, usually inserted on a short cincinnus. *Flowers* mostly small, congested; corollas mostly deeply lobed, white, blue or purplish; filaments often pubescent, the anthers stout, dehiscing introrsely by large, often oblique terminal pores and sometimes ultimately by longitudinal slits in the upper portion; ovary glabrate, the stigma pubescent or not. *Fruit* a berry, mostly juicy; seeds compressed.

Superficially alike in their simple pubescence, lack of armament, and flowers resembling those of *S. nigrum* or *S. americanum*, some of the herbaceous sections in this subgenus (from areas outside of Panama) may later be found to have their true affinities elsewhere, *e.g.* subsect. *Dulcamara* '*Regmandra*' Dun., which resembles species in subgen. *Potatoe*, and sect. *Gonatotrichum* Bitt., the simple hairs of which may be the result of a reduction of stellate hairs as in sect. *Leptostemonum*.

In Panama this subgenus is presented by sections *Solanum* and *Leiodendra*.

N. Section **Solanum.**

Unarmed *herbs*, sometimes subshrubs or epiphytes, glabrate or pubescent with simple hairs; stems often angled, and the angles sometimes forming soft teeth; occasionally sarmentose. *Leaves* simple, mostly ovate, basally truncate or shallowly cuneate, the margins entire or undulate, serrate or dentate; minor leaves often present. *Inflorescence* lateral, mostly a condensed raceme or umbel, the peduncle herbaceous, unbranched or in a few species once-branched, sometimes enlarged at the point of pedicel insertion but the scars themselves not conspicuous. *Flowers* small, perfect, calyx lobed less than halfway, suturing further in fruit, the lobes equal or not, applied to the fruit or reflexed from it, sometimes accrescent in fruit; corolla lobed halfway down or more, white, blue or purple, often with a contrasting eye; stamens subequal, the filaments mostly pubescent

within, the anthers connivent but not connate; ovary glabrous, the style usually pubescent, often thicker in the middle, rarely persistent, the stigma punctiform or rarely 2-lobed. *Fruit* a globose, juicy, many-seeded berry, black (Panama), red, yellow or green; seeds compressed, light-colored, foveolate.

The *Solanum nigrum* complex, as this section is frequently dubbed, is one of the most widespread of solanaceous groups, occurring from Scandinavia to New Zealand and from sea level to over 3,000 m elevation. The taxonomy is complicated by polyploidy, hybridization between taxa, frequency of adventive individuals, a range of plasticity which appears to overlap distinctions between taxa, and the fact that many useful characters are not reliable after drying. The approximately 80 species names published before 1860, and many since, are for the most part supported by fragmentary diagnoses or inadequate illustrations, so that recourse to much type material, mostly scattered in European institutions, is necessary before correct names can be assigned to taxa as they become understood. There may, in fact, be fewer than two dozen species in the section.

This treatment, which recognizes but three species for Panama, is based on a lengthy field and herbarium study of plants from Central and North America and the Antilles as well as greenhouse plants from New Zealand and European seed. Two of the species occur generally from the United States to Panama, and one of these is almost world-wide in distribution. Occasional hybrids may be expected but in Panama, none have been seen by this writer.

The reputation of these plants as foods, medicinal plants, or poisons varies from country to country. Ripe fruits of Panamanian species are apparently edible, but green parts, including fruits and leaves, may be toxic due to their content of solanine group alkaloids. For a critical view of the toxicology of the group, see J. M. Watt and M. G. Breyer-Brandwijk, *The Medicinal and Poisonous Plants of Southern and Eastern Africa* (Edinburgh, 1962). Species occurring in Panama may be troublesome weeds of pastures and cafetales.

Common names are many, and the species are not usually distinguished: "pinta mora" (Panama, Darién), "hierba mora" (Cuba, Mexico, Costa Rica, Colombia, Dominican Republic), "black nightshade" (English).

Although there is a large literature on this section, it is widely scattered in many publications. Dr. Jennifer Edmonds, Cambridge University, has prepared a revision of the South American species (Kew Bull. 27: 95–114. 1972).

a. Anthers less than 1.5 mm (rarely to 2.2 mm) long; calyx strongly reflexed in fruit; pedicels erect in fruit; berries shiny black; occurring from sea level to higher elevations ..... 38. *S. americanum*

aa. Anthers more than 2.2 mm (rarely only 1.7 mm) long; calyx not strongly reflexed in fruit; pedicels deflexed downwards in fruit; berries dull, black or mostly purple; occurring mostly above 1,000 m elevation.

b. Anthers more than 2.9 mm long; fruiting calyx with broadly rounded sinuses, not splitting at the sinuses; peduncles very slender, 2.5 cm or longer ..... 39. *S. macrotonum*

bb. Anthers less than 2.7 mm (rarely to 3.2 mm) long; fruiting calyx with obtuse or acute sinuses, mostly splitting at the sinuses; peduncles stouter, less than 2.5 cm long ..... 40. *S. nigrescens*

38. **Solanum americanum** Mill., Gard. Dict., ed. 8. 1768. TYPE: Authentic specimens Herb. Sloane 295, 14 (BM).—FIG. 25.

S. *nodiflorum* Jacq., Coll. 1: 100. 1788; Ic. Pl. Rar. 2: 17, *tab. 326.* 1786. TYPE: Authentic specimen ex *Jacquin, s.n.* (BM; Bitter, Abh. Naturwiss. Vereine Bremen 23: 138. 1914, also cited a specimen at W, not seen).
S. *triangulare* Lam., Illustr. 2: 18. 1794. TYPE: Herb. *Lamarck s.n.* (P).
S. *parviflorum* Badaro, Giorn. Fis., dec. 2. 7: 364. 1824. TYPE: *Badaro "1824"* (G-DC).
S. *subspathulatum* Sendt. *in* Mart., Fl. Bras. 10: 45–48. 1846. TYPE: Brazil, *Sello s.n.* (P, ex hort. bot. Berol.).
S. *indecorum* A. Rich. *in* Sagra, Fl. Cub. 11: 121. 1850. TYPE: Herb. *Rich. s.n.* (P[40]).
S. *amarantoides* Dun. *in* DC., Prodr. 13(1): 55. 1852. TYPE: Brazil, *Gaudichaud 552* (P, holotype; MPU, isotype).
S. *caribaeum* Dun. *in* DC., Prodr. 13(1): 48. 1852. LECTOTYPE: Jamaica, collector unknown (G-DC ex Kew; F, MO, photos).
S. *fistulosum* Dun. *in* DC., Prodr. 13(1): 49. 1852. LECTOTYPE: Brazil, Herb. Rich. (P).
S. *inops* Dun. *in* DC., Prodr. 13(1): 55. 1852. TYPE: Mexico, *Berlandier 46* (G-DC, holotype; G, P, isotypes).
S. *nodiflorum* var. *acuminatum* Dun. *in* DC., Prodr. 13(1): 46. 1852. LECTOTYPE: Brazil, *Vauthier 537* (P, ex herb. Drake).
S. *nodiflorum* var. *macrophyllum* Dun. *in* DC., Prodr. 13(1): 46. 1852. LECTOTYPE: Brazil, *Gaudichaud 521* (P).
S. *nodiflorum* var. *petiolastrum* Dun. *in* DC., Prodr. 13(1): 46. 1852. HOLOTYPE: Brazil, *Claussen 180* (P).
S. *nodiflorum* var. *puberulum* Dun. *in* DC., Prodr. 13(1): 46. 1852. TYPE: Mexico, *Berlandier 1904* (P).
S. *oleraceum* Dun. *in* DC., Prodr. 13(1): 50. 1852. LECTOTYPE: Cayenna, herb. *Rich. s.n.* (P; MPU, G-DC, isolectotypes).
S. *ptychanthum* Dun. *in* DC., Prodr. 13(1): 54. 1852. TYPE: Georgia, U.S.A., collector unknown (G-DC).
S. *nigrum* var. *nodiflorum* A. Gray, Syn. Fl. N. Amer. 2(1): 288. 1878.
S. *nigrum* var. *americanum* (Mill.) O. E. Schulz *in* Urb., Symb. Antill. 6: 160. 1909–10.
S. *purpuratum* Bitt., Fedde Repert. 13: 85. 1913. TYPE: Andros, Bahamas, *Small & Carter 8805* (P, holotype; US, isotype).
S. *adventitium* Polgar, Magyar Botanicai Lapok 24: 18–22 *tab. 1.* 1925. TYPE: Hungary, *Polgar s.n.* (MPU).
S. *merrillianum* Liou, Contr. Inst. Bot. Nat. Acad. Peiping 3: 455. 1935. TYPE: Hainan, *Tsang 412* (A).
S. *photeinocarpum* Nak. & Odash., Jour. Soc. Trop. Arg. 8: 54. 1936. TYPE: (not seen).
S. *americanum* var. *nodiflorum* (Jacq.) Edmonds, Jour. Arnold Arbor. 52: 634–5. 1971.

Short-lived or annual *herb*, rarely to 1.5 m tall, glabrate or pubescent; stems terete to strongly angled and toothed, often purplish; not sarmentose. *Leaves* small to large (2–20 cm long), entire or mostly somewhat toothed. *Inflorescence* several-flowered, umbellate or nearly so, the peduncle slender, unbranched, appressed-pubescent; pedicels slender, appressed-pubescent, deflexed in bud but erect and spreading in fruit. *Flowers* small, calyx lobes deltoid to lanceolate, not accrescent; corolla white, blue or mauve, with or without a conspicuous eye, small, to 1 cm across; anthers mostly 0.9–1.4(–2.1) mm long. *Fruit* black, shiny, 4–8(–15) mm across; seeds 1.2–1.5 mm across. Chomosome number $n = 12$.

One of the most widespread of all solanaceous species, S. *americanum* is a fairly common weed in Panama and is the only species in this section to be found in lowland areas. It is frequent in gardens, pastures, cafetales, roadsides, and as a street weed.

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[40] This specimen bears two labels. Although the label "Isle de France" is in Dunal's hand, the protologue refers also to the Richard label. The true source of this specimen is not evident.

FIGURE 25. *Solanum americanum* Mill.—A. Habit ($\times \frac{3}{5}$).—B. Flower ($\times 6\frac{3}{5}$). [After *D'Arcy 5448* (MO).]

BOCAS DEL TORO: In wet depression along runway at Bocas del Toro, near houses, *Lazor et al. 2357* (SCZ). Isla Colón, *von Wedel 2840* (GH, MO, US). CANAL ZONE: Fort San Lorenzo, *Burch et al. 1033* (GH, MO, NY). Road S-8, S of Fort Sherman, weedy roadside area, *Croat 12513* (MO). Pan American Highway 2 mi. E of Arraijan, mixed savanna and secondary forest, *Lewis et al. 5183* (MO). Vicinity of Corozal, *Piper 5294* (US). Empire to Mandingo, *Piper 5475* (US). Near Frijoles, *Pittier 6833* (US). Sosa Hill, Balboa, brushy slope, *Standley 25290* (MO, US). Gamboa, old field, *Standley 28440* (US). Balboa, moist woods, *Standley 29252* (US). Vicinity of Summit, weedy field, *Standley 30134* (US). Fort Amador on causeway and islands, *Tyson 2027* (MO). Curundu near Tropic Survival School, *Tyson & Blum 2532* (MO). Macapale Island in Madden Lake, *Tyson 5509* (FSU, MO). CHIRIQUÍ: Between Concepción and El Hato de Volcán, *D'Arcy 4261* (MO). Near Río San Juan, pasture weed, *D'Arcy 4290* (MO). Outskirts of David, grassy area, *D'Arcy 5291* (MO). 6 mi. S of Hato de Volcán, in quarry, 4,800 ft, *D'Arcy 5438* (MO, WIS). Above Boquete, 4,100 ft, *D'Arcy 5448* (F, MO). Boquete, Llano Francia 4 mi. from Boquete toward Dolega, 4,500 ft, llanos bordering creek, *Dwyer & Hayden 7596* (MO, US). Bank of Río Caldero, 10 mi. N of David, *Lazor & Correa 2795* (FSU, MO, SCZ). From Boquete to 3 mi. N, 3,300–4,200 ft, second growth, cultivated areas and roadsides, *Lewis et al. 388* (GH, MO, NY, US). Slopes of Cerro Horqueta, 4,500 ft, *Maurice 860* (US). Vicinity of San Bartolomé, Península de Burica, 50 m, *Woodson & Schery 942* (MO, US). COCLÉ: Las Delicias, *Carleton 227* (US). El Valle ca. 39 km from Interamerican Highway, *Correa 321* (MO, PMA). 12 mi. NE of Penonomé, 1,200 ft, granitic river gorge, *Lewis et al. 1510* (GH, MO, US). Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte, very advanced secondary forest, *Lewis et al. 5545* (MO). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, rain forest, *Porter et al. 4611* (DUKE, MO). COLÓN: Santa Rita lumber road, ca. 15 km E of Colón, forest, *Dressler & Lewis 3735* (MO). Mouth of Río Piedras, beach and adjacent area, *Lewis et al. 3204* (MO). DARIÉN: Vicinity of Boca de Cupe, 40 m, *Allen 876* (MO, US). Near junction Río Peresenico and Río Pirre, scattered plants in fields, *D'Arcy 5533* (MO, W). Río Pirre near crossing of trail from El Real to Tucuti, 20 mi. W of El Real, *Duke 5199* (MO). Río Balsa between Quebrada Chusomocatre and Río Areti, *Duke 8722* (MO, US). Manene to mouth of Río Cuasi, *Kirkbride & Duke 1398* (MO). Manene, *Kirkbride & Duke 1597* (MO). 1 mi. N of Río Sabana, *Tyson et al. 4776* (MO). Boca de Cupe, *Williams 678* (US). LOS SANTOS: Headwaters of Río Pedegral, 25 mi. SW of Tonosí, 2,500–3,000 ft, cloud forest and clearing, *Lewis et al. 2955* (DUKE, MO), *2978* (MO). PANAMÁ: In cafetal, Cerro Jefe, *D'Arcy 3966* (MO). La Chorrera, weed in vacant lot, *D'Arcy 5257* (MO). 5–6 mi. E of Chepo on Pan American Highway, *Duke 4044* (GH, MO). Río Pacora just below confluence with Río Corso, *Duke 12022* (MO). Cerro Jefe, 2,900 ft, forest edge and road bank, *Dwyer & Gauger 7325* (BIRM, C, MO, MPU). Woods near the village, Isla Taboga, *Hjerting & Rahn 2201* (C). Chimán, clearing in rain forest, *Lewis et al. 3299* (MO, NY, PMA). Tributary of Río Chagres, 5 mi. SW of Cerro Brewster, 1,000 ft, sandy and rocky river banks, *Lewis et al. 3398* (DUKE, MO). Near Río Tapia, Juan Díaz region, dense shade along stream, *Maxon & Harvey 6711* (US). 1 mi. N of Goofy Lake, edge of cultivated field, *Oliver et al. 2677* (DUKE, MO). Cerro Azul, roadside woods and thickets, *Porter et al. 4067* (MO). Vicinity of Arenoso, lower Río Trinidad, 26–50 m, *Seibert 601* (MO, NY). Río Tapia, wet forest, *Standley 26213* (US). Taboga Island, moist thicket, *Standley 27092* (US). Río Tapia, brushy slope, *Standley 28117* (US). 3 mi. E of El Llano at Finca Risso, *Tyson 1732* (MO). Cerro Azul, 2,000 ft, in sun, *Tyson 2136* (MO). Taboga Island near village, *Tyson & Loftin 5103* (FSU, MO). SAN BLAS: Soskatupu, island ca. 1.5 mi. long, *Elias 1671* (DUKE, MO). Mainland opposite Achituppu, from beach to 1.5 mi. inland, marshy rain forest often by native plantations, *Lewis et al. 93* (MO). VERAGUAS: Just west of Santiago, weedy roadside, *D'Arcy 5272* (MO).

39. **Solanum macrotonum** Bitt., Fedde Repert. 11: 222. 1912. TYPE: Venezuela, *Moritz 1643* (P).

S. *guineense* Lam., Illustr. 2: 18. 1794, non L., Sp. Pl. 184. 1753. TYPE: Herb. *Lam. s.n.* (P).
S. *diodontum* Bitt., Fedde Repert. 12: 552. 1913. TYPE: Panama, *Pittier 3104* (GH, NY, US).

Scandent *herb*, stems glabrescent, the nodes distant. *Leaves* moderate-sized, 5–8 cm long, margins repand with 1–2 small teeth just below the middle, young leaves copiously pubescent, older leaves with sparse scattered hairs above; petioles

winged about ½ as long as the leaves. *Inflorescence* umbellate, appressed-puberulent with ascending hairs, the peduncle straight and very slender, 2–3 cm long; pedicels flexuous, slender but slightly expanding over the whole length, 12–18 mm long. *Flowers* white, calyx 3 mm long and 3 mm across the top, obconical, with short, deltoid teeth and curved sinuses which do not split in flower or fruit; corolla 10 mm long, lobed more than halfway; anthers ca. 3 mm long; the style filiform, curved in the upper ⅓, slightly exserted. *Fruit* ca. 6 mm across, the calyx slightly accrescent, mostly neither applied nor reflexed but almost porrect around the fruit; seeds ca. 1.3 mm across. Chromosome number $n = 36$.

This species is best recognized by its large anthers and fruiting calyx, as well as by the slender appearance of stems and inflorescences. It is not always easily distinguished from S. *nigrescens*. The anther length (3 mm) given here (taken from *Pittier 3104*) is not attained by Panamanian specimens of S. *nigrescens* and is seldom attained by that species from other areas. I am grateful to Dr. J. Edmonds, University of Cambridge, for providing the name and the chromosome number of this species.

In Panama, this species occurs at upper elevations along stream banks, often within the spray of waterfalls.

CHIRIQUÍ: Around El Potrero Camp, Chiriquí Volcano, 2,800–3,000 m, humid ravine, trailing on shrubs, *Pittier 3104* (GH, NY, US). Trail through Paseo de Respinga on way to Boquete, 7,500 ft, *Wilbur & Teeri 13156* (DUKE). Vicinity of Bajo Chorro, 1,900 m, *Woodson & Schery 635* (MO, taxonomic placement uncertain, the anthers are 3.4 mm long).

40. **Solanum nigrescens** Mart. & Gal., Bull. Acad. Roy. Brux. 12(1): 140. 1845. TYPE: *Galeotti 1238* (P).

S. *aloysiaefolium* Dun. *in* DC., Prodr. 13(1): 73. 1852. HOLOTYPE: Bolivia, *d'Orbigny 1208* (P).
S. *crenato-dentatum* Dun. *in* DC., Prodr. 13(1): 54. 1852. LECTOTYPE: San Fernando, Chile, *Gay s.n.* (P); paratype, Mexico, *Berlandier 118* (G).
S. *crenato-dentatum* var. *ramossissium* Dun. *in* DC., Prodr. 13(1): 54. 1852. TYPE: Louisiana, *Barbe ?s.n.*, 1839 (P).
S. *gracile* Dun. *in* DC., Prodr. 13(1): 54. 1852, non S. *gracile* Sendt. *in* Mart. Fl. Bras. 10: 13. 1846. TYPE: Hort. Monsp. 1831 (MPU) (= S. *gracile* Link, nomen nudum).
S. *douglasii* Dun. *in* DC., Prodr. 13(1): 48. 1852. TYPE: California, *Douglas 1833* (BM, G-DC, ?K, MPU, P).
S. *nigrum* var. *rigidum* Dun. *in* DC., Prodr. 13(1): 50. 1852. LECTOTYPE: Specimen labelled manu Dunal "1841–1847" (P).
S. *durangoense* Bitt., Fedde Repert. 12: 82. 1913. TYPE: Mexico, *Palmer 101* (US).
S. *approximatum* Bitt., Fedde Repert. 12: 86. 1913. TYPE: Jamaica, *Nichols 89* (MO, US).

Perennial *herb*, rarely to 3 m tall, sometimes epiphytic; stems terete to angled, often purplish; often sarmentose. *Leaves* to 10 cm long but mostly much shorter, ovate to lanceolate, entire or toothed. *Inflorescence* a condensed raceme or umbellate, 1- to several-flowered; the peduncle slender, appressed pubescent; pedicels slender, often thickening in fruit, appressed-pubescent, erect or deflexed in flower but always strongly deflexed in fruit. *Flowers* with the calyx lobes ovate, lanceolate or deltoid, not accrescent; corolla white or mauve, mostly with a conspicuous eye, small (to 15 mm across); anthers mostly 2.5–2.9 mm long. *Fruit* black or rarely green with dark purple markings, dull, mostly 4–8 mm across; seeds 1.2–1.5 mm across. Chromosome number $n = 12$.

This species is widespread in the New World, ranging from Bolivia north to California and North Carolina. In California and Florida, where it is common, it is typically a coastal plant seldom exceeding 70 cm except in the extreme south of these states. Further south it becomes a very large herb, sometimes exceeding 2 m in height. In the tropics it is restricted to middle or perhaps upper elevations. In Panama, the species is plentiful in the Volcán and Boquete districts, where it is a common plant of cafetales and mountain pastures.

Solanum nigrescens is quite like *S. nigrum* L. (which does not occur in Panama) in general appearance but differs in the more slender peduncle and pedicels, the diploid condition, smaller seeds, and its tropical range.

It is likely that an earlier name will be found for this species; either because a type may be found to support an earlier name for plants like those of California, Mexico, and Panama, or because a decision is evolved to include plants of *S. chenopodioides* Lam.[41] and *S. nigrescens* within the same species concept. *Solanum pygmeum* is a name for plants of northern Argentina and southern Brazil, usually recognizable by smaller, sinuately lobed and thicker leaves than are usual on *S. nigrescens*, but some collections are difficult to assign between these species concepts.

CANAL ZONE: Empire to Mandinga, *Piper 5475* (US). CHIRIQUÍ: Nueva California, *D'Arcy 4245A*, *4251*, *4253B* (all MO). Los Naranjos, in cafetal, *D'Arcy 4267*, *4271* (both MO). Vegetable fields above Nueva Suisa, Volcán district, 6,000 ft, *D'Arcy 5328* (BIRM, MO). Above Boquete in pasture area, 5,200 ft, *D'Arcy 5461* (ADW, MO, RSA). Bajo Chorro, Boquete District, rain forest, 6,000 ft, *Davidson 183* (A, MO, US). Vicinity of El Boquete, 1,000–1,300 m, weed in coffee plantation, *Maxon 5164* (US). Boquete, *Seeman 1606* (BM, K). Potrero Muleto to summit, Volcán de Chiriquí, 3,500–4,000 m, terrestrial, flowers white, *Woodson & Schery 464* (MO). DARIÉN: Boca de Cupe, *Williams 678* (US).

O. Section **Leiodendra** Dun., Sol. Syn. 20. 1816. LECTOTYPE: *S. diphyllum* L.

Shrubs or *trees*, mostly glabrate with inconspicuous or localized simple hairs, but sometimes manifestly pubescent; stems woody, terete or angled. *Leaves* entire, mostly short-petioled but not sessile, minor leaves often present, smaller and more rotund than the major leaves. *Inflorescences* few or several, more or less opposite the leaves, mostly secund, congested or subumbellate on a short lignified peduncle, the peduncle mostly little-branched, often elongating and becoming woody in fruit, mostly with a conspicuous cicatrix of pedicel scars which are sometimes enlarged and elevated; pedicels slender but often larger, thicker, usually woody in fruit. *Flowers* small, calyx small and sometimes somewhat accrescent but never greatly so; corolla distinctly lobed; filaments not strongly unequal, the anthers stout, opening by large, introrse terminal pores, connivent but not connate; ovary essentially glabrous. *Fruit* a globose, juicy or

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[41] *Solanum chenopodioides* Lam., Illustr. 2: 18. 1794 [TYPE: Commerson, Buenos Aires (P; an examination of the suite of specimens at Paris (P) and Montpellier (MPU), leads to the conclusion that Lamarck was describing Commerson plants from Buenos Aires, and his mention of a Mauritius (or Île de Bon) specimen is irrelevant)], includes *S. pygmeum* Cav., Icones 5: 23, *t. 439*, f. 2. 1799 [TYPE: Laguna de Ballestero, pampas de Buenos Aires, *Nee iter s.n.* (MA)]; *S. sublobatum* Willd. *ex* R. & S. *in* L., Syst., Veg. 4: 664. 1819 [TYPE: Buenos Aires, Herb. *Willd. 4336* (B, not seen; IDC 7440, 298 II. 2)]. This species often, but by no means always, blooms when very small, less than 15 cm tall.

fleshy berry, many-seeded, ripening yellow-orange or perhaps black; seeds somewhat compressed, small, light-colored, foveolate.

This section comprises mostly forest species of tropical America, although a few are found in disturbed habitats. Remarkably uniform on the herbarium sheet, species are distinguished on nice distinctions of pubescence, pedicel shape and other characters often overlooked. Many dozens of species may exist.

Section *Leiodendra* is usually easy to recognize by the woody habit and the prominent cicatrix of pedicel scars. In other details, plants are very similar to those of sect. *Solanum*, although in that section, inflorescences soon become lateral by moving to positions between the nodes. The section also bears a close similarity to the genus *Cyphomandra*, which is distinguished by enlarged anther connectives and inflorescences at dichotomies of the stem.

Three collections of Solanaceae from Panama that may belong to sect. *Leiodendra* have not been assigned to species. They may at some time be assignable to species described here or they may represent species new to Panama. In view of the great variability of plants in the family, it seems unwise to describe them as new:

1. *Dwyer & Hayden 7750* (MO). This specimen has large, broadly elliptic and strongly oblique leaves and one detached fruiting peduncle. The peduncle is glabrous, very slender, divided ca. 9 cm above the base into two unequal branches, 15–40 mm long, each terminated with a short cicatrix and each bearing a single slender, 30 mm pedicel and globose or slightly flattened berry ca. 8 mm across. It may belong in this section or might be a species of *Cyphomandra*. Label information reads: "Boquete, Cerro Horqueta, 5,000–6,000 ft, dense woodland in cloud forest, shrub to 2 m., Chiriquí Province."

2. *Hagen & Hagen 2084* (MO). This specimen may be an extreme variant of *Solanum rovirosanum*. The specimen is in fruit. The leaves are large, 30 cm long, and the inflorescences are opposite the leaves. The peduncles are stout, less than 5 mm long and perhaps once branched. The pedicels are moderately stout, 20 mm long. Label information reads: "Cerro Horqueta, cloud forest, 6,500 ft, tree 10 ft, Chiriquí Province."

3. *Stern et al. 661* (GH, MO, US). This collection is in fruit. Quite like S. *arboreum*, the collection has membranaceous leaves, and the pedicels are slender. It may be related to S. *conicum* Dun. of Peru. Label information reads: "Vicinity of Caná, 1,750 ft, small shrub, 24 inches high, ⅜ inch diameter, in fruit, Darién Province."

a. Leaf undersides mostly with tufts of hairs in the vein axils, otherwise glabrate; fruiting pedicels slender, if thickening apically then not much elongating.
  b. Flowering calyx glabrous; leaf undersides glabrous except in the vein axils; flowers usually drying yellowish; fruiting pedicels slender ..... 41. S. *antillarum*
  bb. Flowering calyx with long white hairs near the apex; leaf undersides often with hairs on the lamina near the main veins; flowers often drying with a purplish cast; fruiting pedicels thickening apically ..... 47. S. *nudum*

aa. Leaf undersides glabrous or pubescent but without tufts of hairs in the vein axils; fruiting pedicels thickening or if not then greatly elongating.
  c. Peduncle elongating to 3–10 cm, the pedicel scars well spaced.
    d. Leaf lamina copiously pubescent beneath ..... 44. S. *eshbaughianum*
    dd. Leaf lamina mostly glabrous.

e. Leaves pubescent at the veins, fruiting pedicels more than 2 mm long with a conspicuous swelling near the apex ..... 43. S. *coibae*
ee. Leaves glabrous overall, fruiting pedicels less than 2 mm long, slightly expanded but without a conspicuous swelling near the apex ..... 48. S. *rovirosanum*

cc. The peduncle not much elongating in fruit, mostly less than 3 cm long, the pedicel scars mostly congested.
f. Leaf undersides glabrous or finely puberulent.
g. Peduncles mostly once-branched; fruiting pedicels slender (woody) ..... 46. S. *intermedium*
gg. Peduncles mostly unbranched; fruiting pedicels stout (woody) ..... 42. S. *arboreum*
ff. Leaf blades manifestly pubescent beneath, more densely so near the veins ..... 45. S. *incomptum*

41. **Solanum antillarum** O. E. Schulz *in* Urb., Symb. Antill. 6: 164–166. 1909–10. SYNTYPES: Cuba, *Eggers 5039* (P); Cuba, *Wright 388* (P); Grenada, *Eggers 6072* (MPU, P).—FIG. 26.

S. *tovarense* Bitt., Fedde Repert. 18: 65. 1922. TYPE: Venezuela, *Fendler 980* (MO, NY).
S. *parcebarbatum* Bitt., Fedde Repert. 18: 51–52. 1922. SYNTYPES: Costa Rica, *Tonduz 9018, 11491* (both US), Panama, Canal Zone, Alhajuela, *Pittier 2325*, near Gatun, *Pittier 2653* (both US).

Shrub or *tree* to 3 m tall; twigs mostly drying smooth dark brown, terete or angled. *Leaves* 8–15 cm long and 4–8 cm broad, lanceolate to broadly elliptical, widest about the middle, mostly acuminate but sometimes obtuse or acute apically or basally, glabrous except for usually conspicuous tufts of white hairs in the vein axils beneath; minor leaves conspicuous, ⅓–½ as large as the majors, basally mostly acuminate. *Inflorescences* several, mostly near the ends of the twigs, subumbellate on a slender, usually short, unbranched peduncle bearing a conspicuous contracted or scattered cicatrix; pedicels filiform, thickening towards the apex, mostly less than 1 cm long, in fruit becoming somewhat stout toward the apex but remaining slender at the base. *Flowers* with the calyx glabrous, buttonlike in bud, the lobes not quite enclosing the bud, becoming deltoid and splitting at the sinuses as the corolla emerges, in fruit enlarging only slightly and the lobes appearing obtuse or rounded; corolla white, often drying greenish-yellow or sometimes brownish-yellow, 3–4 mm long, lobed ⅓–½ way down; anthers 1.8–2.8 mm long. *Fruits* to 1 cm across.

This species may be recognized by the small, tightly compacted flowers and the button-like buds as well as by the pilose vein axils and large minor leaves. The yellowish color of the dried flowers is often indicative.

Solanum antillarum ranges from Mexico to Venezuela and perhaps beyond. It occurs on many of the Antillean islands, where the fruits are slightly smaller than those in Panama. In Panama it is known mainly from the central part of the country, growing in moist forests and roadsides at lower elevations. Most collections are from the slopes of Cerro Pilón near El Valle de Antón, Coclé Province.

CANAL ZONE: Barro Colorado Island, *Aviles 72, 555* (both MO). Along stream, Madden Forest Road No. 2, *Croat 8958* (MO). Road S-11 NW of Escobal, *Croat 12455* (MO). Pipeline road near gate, *Croat 13940* (MO). Barro Colorado Island, rear lighthouse clearing No. 8, *D'Arcy 3988* (MO). Madden forest, side of disused gravel road, 200 m, *D'Arcy 5243* (ADW, BIRM, MO, MPU). Gatún Station, Panama Railroad, *Hayes 144* (NY). Cove N

FIGURE 26. *Solanum antillarum* O. E. Schulz, habit (× 3/5). [After *D'Arcy 5243* (MO).]

of Drayton House, *Woodworth & Vestal* 555 (MO). CHIRIQUÍ: Above Paseo la Canoa, 3,000 ft, *D'Arcy 5431* (MO). COCLÉ: Near El Valle, 800–1,000 m, *Allen 101* (A, MO), *1199* (GH, MO, NY, US). Near La Mesa in cloud forest, *Croat 13331* (MO). Flat forested area below Cerro Pilón, *Croat 13437* (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12058, 12104* (both MO). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7943* (C, F, MO, MPU, UCWI), *7970A* (MO, PMA). Cerro Pilón, 2,700 ft, *Dwyer & Lallathin 8614* (ADW, MO, MPU). El Valle de Antón, 500 m, lower portions of valley and marshes along Río Antón, *Hunter & Allen 368* (MO). El Valle de Antón, 1,000–2,000 ft, edge of cloud forest and roadside, *Lewis et al. 2516* (MO). Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte, very advanced secondary rain forest, *Lewis et al. 5522* (MO), *5570* (MO, MPU). El Valle, valley floor and lower slopes along highway, *Miller 1835* (US). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, rain forest, *Porter et al. 4580, 4604* (both MO). Mountains above El Valle, bushes beside dirt road in mountains, *Stimson 5014* (DUKE, PMA, SCZ). Between Las Margaritas and

El Valle, *Woodson et al. 1276* (A, MO, NA, NY). PANAMÁ: Without locality, *Hayes 299, 753* (both NY). VERAGUAS: Tute, *Dwyer 4313* (MO).

42. **Solanum arboreum** H. & B. *ex* Dun., Sol. Syn. 20. 1816. TYPE: Venezuela, *Bonpland s.n.* (P; IDC 6209. 61. I. 6).

S. novo-granatense Dun. *in* DC., Prod. 13(1): 680. 1852. TYPE: Colombia, *Linden 834* (G-DC).
S. anisophyllum Van Heurck & Müll.-Arg., Obs. Bot. 52. 1881. TYPE: Peru, *Spruce 4830* (G, GH).
S. loretoanum Bitt., Fedde Repert. 18: 70. 1922. TYPE: Peru, *Ule 6277* (G).
S. kenoyeri Standl., Publ. Field Columbian Mus., Bot. ser. 4: 157. 1929. HOLOTYPE: Panama, *Kenoyer 515* (US-1317601).
?*S. orygale* Mort., Contr. U. S. Natl. Herb. 29: 53. 1944. HOLOTYPE: Colombia, *Haught 2850* (US).
S. deflexiflorum var. *diversum* Macbr., Field Mus. Nat. Hist., Bot. ser. 13: 203. 1962. TYPE: Peru, *Mexia 6261* (US).

Shrub or *tree* to 8 m tall; twigs slender or stout, often with finely flaking bark or corky lenticels. *Leaves* 4–20 cm long and 2.5–10 cm broad, broadly elliptical to lanceolate, apically short acuminate to acute, basally narrowed or rounded, glabrous or with some minute puberulence along the major veins beneath, not more pubescent in the vein axils; petioles 0.5–2 cm long, slender or quite stout; minor leaves mostly present, rotund, 2–5 cm long. *Inflorescences* subumbellate on a short, to 1.5 cm long, unbranched peduncle usually becoming stout in fruit and bearing lines of closely and evenly spaced large pedicel scars for much of its length; pedicels filiform, to 10 mm long, in fruit becoming quite stout but not greatly elongating. *Flowers* opposite the leaves but carried along the underside of the horizontal branches well beneath the foliage; calyx almost enclosing the greenish-white bud, the lobes slightly unequal, short deltoid, often puberulent at the tips, and slightly but evidently recurved outwards from the floral axis, splitting at the sinuses as the corolla begins to emerge, developing a constriction at the base of the lobes which in fruit gives the lower part of the calyx a conspicuous bulge or an apparent thickening; corolla white, drying yellowish to russet brown, 4 mm long, lobed nearly to the base; anthers 1.8–2.8 mm long. *Fruits* to ca. 1.2 cm across.

This species is best distinguished by the short, stout fruiting pedicels, the absence of hairs in the vein axils, and in the field by the horizontal orientation of the young branches.

Solanum arboreum is an understory species of mature forests, often occurring on densely shaded slopes. It ranges from Venezuela to Mexico and Peru. More than one species may be present in material now considered to be *S. arboreum*. Material from central Panama is quite uniform.

BOCAS DEL TORO: Lincoln Creek, *Carleton 85* (US). Río Changuinola near Changuinola, *Dwyer 4399* (MO). Between Buena Vista coffee finca and Cerro Pilón on Chiriquí Trail, cloud forest, *Kirkbride & Duke 705* (MO). Between Quebrada Gutierrez and E slope of La Zorra, headwaters of Río Mali, on Chiriquí Trail, *Kirkbride & Duke 722* (MO). Chiriquicito to 5 mi. S along Río Guarumo, rain forest by river, *Lewis et al. 2122* (MO). Punta Pena, vicinity of Chiriquicito, 1,000 ft, rain forest, *Lewis et al. 2167* (MO, P). Almirante, near Nigra Creek, *McDaniel 5069* (MO). Vicinity of Chiriquí Lagoon, Fish Creek Mountains, *Wedel 2268, 2367* (both GH, MO, US). Vicinity of Chiriquí Lagoon, Changuinola River,

Wedel 2603 (GH, MO, US). Vicinity of Nievecita, *Woodson et al. 1828* (MO). CANAL ZONE: Pipeline road, 2½ mi. from gate, *Croat 9352* (DUKE, MO, NY). Pipeline road ½ mi. N of gate, N of Gamboa, *D'Arcy 5208, 5210* (both MO). Madden Forest Preserve, along Las Cruces Trail and highway, deep rain forest, *Lewis et al. 5326* (ADW, BIRM, C, F, MO, MPU, PMA, UCWI). Indio, Madden Lake, *Miller 2046* (US). Cuatro Calles Hills, near Matachin, 20–150 m, *Pittier 4048* (US). 12 mi. S of Colón on Río Providencia, *Tyson & Blum 3944* (FSU, MO). Barro Colorado Island, *Bartlett & Lasser 16740* (MO); *Croat 6680, 6768, 10119* (all MO), *Croat 11151* (MO, NY); *D'Arcy 4296* (MO); *Killip 39986* (US); *Standley 31358, 41143* (both US); *Starry 112* (G), *291* (MO). CHIRIQUÍ: In forest above Boquete, 5,200 ft, *D'Arcy 5476* (MO). Cerro Horqueta, cloud forest, 5,000–7,000 ft, *Kirkbride 135* (MO, SCZ). COCLÉ: Hills NE of El Valle de Antón, 2,000 ft, disturbed forest edges, *Lewis et al. 1690* (MO). DARIÉN: Vicinity of Pinogana, 20 m, *Allen 930* (GH, MO, NY, US). Río Uruceca, *Bristan 1445* (MO, WIS). Along Pan American Highway between Pucro and Río Punusa, *Duke 5402* (MO). Cerro Pidiaque, *Duke 8083* (MO, WIS). Quebrada Nigua, *Duke 8826* (MO, WIS). Aqua Fria 8 mi. N of Santa Fé, 50 m, *Duke 10111* (MO, WIS). Cerro Pirre, 2,500–4,500 ft, cloud forest and/or mossy forest, *Duke & Elias E13669* (C, MO, W). Between Paya and Palo de las Letras, *Duke & Kirkbride 14029* (MO). Río Sabana above Santa Fé, *Duke 14080* (MO). Tumaganti, 300 m, *Duke 14145* (MO). Manene to mouth of Río Cuasí, *Kirkbride & Bristan 1536* (MO). Near Caná, 1,750 ft, in understory of second growth forest at old town of Caná, *Stern et al. 498, 696* (both GH, MO, US), *477* (MO), *661* (GH, MO, US). Marraganti, *Williams 791* (US). LOS SANTOS: Headwaters of Río Pedregal, 25 mi. SW of Tonosí, 2,500–3,000 ft, cloud forest and native clearing, *Lewis et al. 2888* (MO). Between Tonosí & Guanico, scraps of forest along trail containing large espaves, *Stern et al. 1886* (MO, US). 10 mi. N of Tonosí, *Tyson et al. 2949* (MO, SCZ). 1 mi. N of Tonosí, *Tyson et al. 2987* (MO). PANAMÁ: Cerro Campana, *Allen 2088* (MO), *Croat 12072* (MO), *D'Arcy & Dressler 5493* (BIRM, MO, W), *5506* (MO, W). Near Río Bayano dam ca. 5 mi. S of Cañitas, on spoil bank, *D'Arcy & Croat 5191* (BIRM, MO, P, PMA). Along Pan American Highway, open grazed area near Jenine, Río Cañita, *Duke 3873* (GH, MO, US). Between El Llano and Río Mamoni, woods along Pan American Highway, *Duke 5562* (MO). Forests along headwaters of Río Corso, 500 m, *Duke 11924* (MO, WIS). Piria-Cañasas trail near Piria, 100 m, *Duke 14332* (MO, WIS). Cerro Campana, ¾ of the way to summit from Pan American Highway, *Dwyer et al. 4701* (MO). Junction Río Pacora & Río Corso to headwaters of Río Corso, rain forest, *Oliver 2377* (MO). Cerro Campana above Su Lin Motel, rain forest, *Porter et al. 4274* (MO). SAN BLAS: Headwaters of Río Mulatupo, seasonal evergreen forest, *Elias 1774* (MO). Forests around Puerto Obaldía, 0–50 m, *Pittier 4287* (US).

43. **Solanum coibae** Riley, Kew Bull. 1927: 125. 1927. TYPE: Coiba, Panama, *Collinette 473* (BM, US).

Robust *shrub* 2–4 m tall; twigs smooth, glabrous, fistulose. *Leaves* to 20 cm long, broadly elliptical, acute or rounded apically and basally, glabrous above, glabrous beneath except for long hairs emerging from between the midrib and the leaf lamina, hairs not noticeably denser in the vein axils, membranaceous, drying with a yellowish cast; petioles 2–5 cm long, flexuous; minor leaves when present rotund, ca. 3 cm long and short-petiolate. *Inflorescence* glabrous, opposite the leaves, an unbranched, congested raceme on a short, 15 mm long, peduncle which in fruit may more than double in length and the raceme axis become elongate to 4 cm long with large, conspicuous, widely spaced pedicel scars; pedicels filiform, 15–18 mm long, in fruit becoming 3 cm long, near the base slender and curved, apically clavate and forming an almost globose, woody swelling, 4 mm across. *Flowers* large for this section, calyx 3 mm long and not enlarging in fruit, nearly truncate with a sinuate-lobed apex; corolla white, 2 cm across, lobed to ¾ the way down, the lobes thick, narrowly deltoid; stamens (Riley) connate into a very short tube ca. 0.25 mm high, the filaments hardly 0.25 mm long and almost 0.5 mm broad, the anthers oblong, 5.5 mm long, obtuse, with 1 mm long apical

pores. *Fruit* ca. 15 mm across, drying very wrinkled, the pulp (*Dwyer 1554*) brown; seeds numerous.

This species is glabrous except for the hairs along the leaf midvein beneath. The long flowering pedicels, large flowers, elongating peduncle and rachis, and the appearance of the fruit and its pedicel are distinctive.

Solanum coibae is interesting in having the hairs of the leaf tucked between the midvein and the lamina and apparently not on the midvein itself. The hairs are not particular to the vein axils. The Dwyer specimens are all in fruit. The Collinette specimen (US) has one open flower pasted face down against the herbarium sheet, and particulars of the androecium or gynoecium were not reexamined.

VERAGUAS: Coiba, edge of jungle, flowers white, yellow center, *Collinette 473* (BM, US). Isla de Coiba, *Dwyer 1554* (MO, SCZ, US).

44. **Solanum eshbaughianum** D'Arcy.[42] Holotype: PANAMA, *Pittier 6695* (US-716751).—FIG. 27.

Shrub; twigs puberulent, smooth with conspicuous stipular ridges on the terete surface, glabrescent. *Leaves* to 16 cm long, broadly elliptical or oblong, upfolded from the slightly recurved midvein, apically short-acuminate, basally rounded or obtuse, and dimidiate with one side sometimes acuminate, glabrous above, beneath pubescent, especially on the edges of the veins, lateral veins 7–12 on each side, elevated beneath; petioles 2–3 cm long, almost terete with a channel at the very top, puberulent; minor leaves almost ½ as long as the majors, rotund, sessile or short-petioled. Inflorescences numerous, opposite the leaves or lateral, congested, slender racemes, the peduncle unbranched, 3–5 cm long with conspicuous, elevated pedicel scars, glabrous; pedicels very slender, 1–2 cm long, glabrous, elongating somewhat in fruit. *Flowers* large and unusual for this section, calyx glabrous, ca. 2 mm long, lobed about halfway down, the lobes obtuse with mucronulate tips; corolla with stout thick lobes distinct to the base but united by membranaceous plicae almost halfway up, the lobes and plicae perhaps of different colors; stamens equal, the filaments united for most of their length but not running into an expanded connective, the anthers oblongoid, slightly tapered, opening by large terminal pores which are confluent with short, subapical longitudinal slits; ovary conical, glabrous, the style exceeding the anthers but not the corolla lobes, the stigma lateral on the slightly swollen style apex. Fruit not seen.

Superficially much like S. *leucocarpum* Dun. of the Guyanas or like S. *patellare* Van Heurck & Müll.-Arg. of eastern Peru, this species differs in being

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[42] *Solanum eshbaughianum* D'Arcy, spec. nov. Frutex, ramunculis puberulentibus pilis simplicibus, glabrescentibus; folia jusque ad 16 cm longa, late elliptica vel oblonga, apice breve acuminata, base rotunda, obtusa vel dimidiata, supra glabra, infra pubescentia, praesertim lateribus venorum, venis lateralibus 7–12 utroque, infra elevatis; inflorescentiae numerosae, oppositifoliae vel lateralis, pedunculis haud ramosis, 3–5 cm longis, cicatricem conspicuam gerentibus; flores magni, calyce glabro, 2 cm longo statu fructu aliquot accrescenti, lobis obtusis, mucronulatis, corolla lobis imo crassis membrana plicata conjunctis, staminibus aequalibus, filamentis connatis, antheris oblongatis, ovario conico, glabro; acini haud suppetunt.

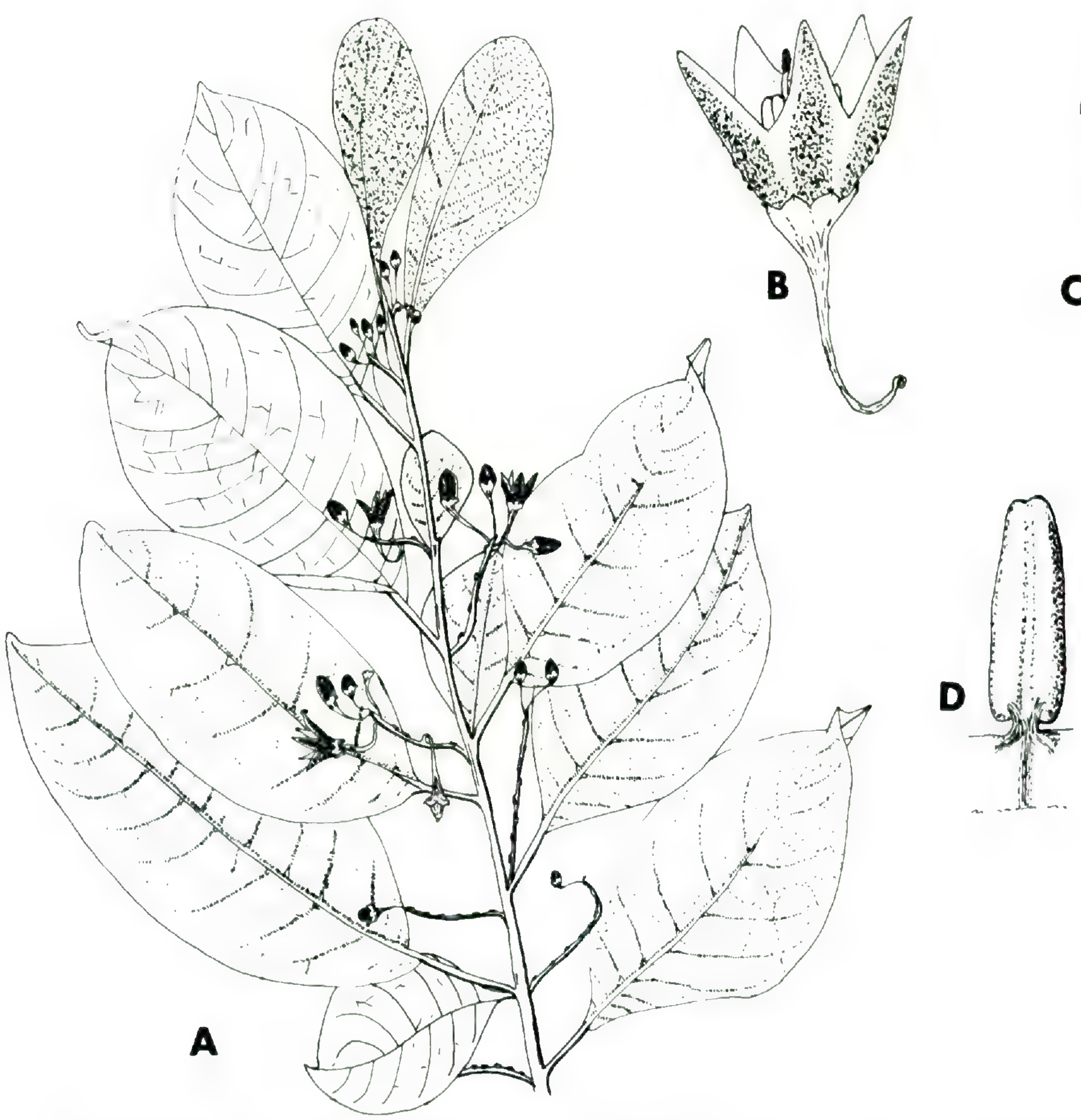

FIGURE 27. *Solanum eshbaughianum* D'Arcy.—A. Habit (× ½).—B. Flower (× 2).—C. Androecium and part of gynoecium, the perianth removed (× 2).—D. Stamen, dorsal view (× 7). [After *Pittier 6695* (US).]

manifestly pubescent on the leaf undersides and in most of the inflorescences being lateral. Of clear affinity to section *Leiodendra*, where it is here placed, it has a good resemblance to *Cyphomandra*, lacking, however, the expanded anther connective characteristic of that genus.

It is known only from the type collection.

DARIÉN: Vicinity of La Palma, 0–50 m, *Pittier 6695* (US).

45. **Solanum incomptum** Bitt., Fedde Repert. 18: 60–61. 1922. TYPE: Costa Rica, *Tonduz 1468* (US).

Shrub or small *tree* to 4.5 m tall; twigs soon glabrescent. *Leaves* 7–15 cm long, lanceolate to broadly ovate or elliptic, narrowed or obtuse, apically and basally, the margins slightly revolute, glabrous to sparsely pilose above, beneath with scattered straight hairs on the lamina and pilose along the midveins and the lamina near it; petioles 1–2 cm long; minor leaves very variable, from small and rotund-auriculate to almost equalling the majors, sometimes wanting. *In-*

florescence mostly opposite the leaves but sometimes appearing axillary or lateral, a subumbellate raceme on a short, unbranched or sparingly branched peduncle, not elongating in fruit; pedicels filiform, 4–6 mm long, elongating to 15 mm and stiffening in fruit. *Flowers* with the calyx glabrous, 1–2 mm long, mostly with minute but distinctly acuminate teeth, splitting before the corolla emerges or later, in fruit to 10 mm across and the lobes appearing deltoid; corolla greenish-white, ca. 12 mm across, lobed nearly to the base; anthers 2–4 mm long, dehiscing by large terminal pores. *Fruit* globose, to 1 cm across.

Solanum incomptum is recognizable by the general pubescence on the leaf undersides and the short, woody peduncles. The glabrous calyces are distinct from those of S. *micranthum*, which may also have pubescent leaf undersides and which occurs in the same district.

CHIRIQUÍ: Bajo Chorro, Boquete District, rain forest, 6,000–7,000 ft, *Davidson 99, 446* (both A, MO, US). Valley of the Río Chiriquí Viejo N of Volcán City, 5,200–5,600 ft, *Duke 9011* (MO, WIS). 6 mi. NE El Volcán, in deep moist canyon bottom, 7,000–7,500 ft, *Tyson 812, 814* (FSU, MO). Cerro Punta, 6,000 ft, *Tyson 5819* (FSU, MO, SCZ). Río Chiriquí Viejo valley near Cerro Punta Gate, *White 51* (GH, MO, US).

46. **Solanum intermedium** Sendt. *in* Mart. Fl. Bras. 10: 22. 1846. TYPE: Brazil, *Martius s.n.* (M, not seen; MO, photo).

S. *dolichostylum* O. E. Schulz *in* Urb., Symb. Antill. 6: 158–159. 1909–10. TYPE: Tobago, *Eggers 5797* (A, K, MPU, P, US).

S. *imberbe* Bitt., Fedde Repert. 18: 62–64. 1922. HOLOTYPE: Panama, *Pittier 4204* (US); paratype 4735 (US).

S. *aquatile* Mort., Contr. U. S. Natl. Herb. 29: 50. 1944. TYPE: Colombia, *Haught 1868* (A, US).

Shrub to 2 m tall; twigs glabrous, drying with a glaucous appearance. *Leaves* 8–20 cm long and 1.5–8 cm wide, elliptical to narrowly lanceolate, mostly widest at the middle or above, the base and apex acuminate, basally sometimes narrowed almost to the base of the petiole, mostly glabrous but sometimes with fine, minute hairs along the principal veins. *Inflorescences* opposite the leaves but sometimes aggregated near the ends of the branches and appearing terminal, the peduncle simple or once-branched ca. 1 cm above the base, the fallen flowers leaving a congested or scattered cicatrix; pedicels filiform, in flower aggregated to appear umbellate, to 1 cm long but mostly shorter, in fruit thickening, elongating and stiffening but not becoming stout, the thickening even along the length. *Flowers* small, the young calyx almost enclosing the bud and bearing short but distinct teeth, glabrous, splitting deeply at the sutures before corolla emergence, the margins becoming irregular and indistinct, not much enlarging in fruit; corolla white, often drying a yellowish-orange, ca. 5 mm long, lobed nearly to the base; anthers oblongoid, 2–3 mm long. *Fruits* ca. 8 mm across.

Solanum intermedium is usually distinguishable by its forked peduncles, glabrous leaves and the orange-yellow corolla of dried material. This is a plant of river banks and gravel bars and assumes the habit common for willows (*Salix*) on flood plains in North Temperate regions. The species ranges from Mexico to Peru and Trinidad.

Panamanian material displays a nearly or complete absence of minor leaves,

which are conspicuous on some South American plants. When minor leaves are present as in *Pittier 4204*, they are lanceolate and small, not large and obovate as in *Eggers 5797* from Tobago. *Haught 1868* from Colombia has a striking grey-green, smooth appearance to the leaves but is otherwise like Panamanian material. Although a wide ranging species, Panamanian collections are mostly from eastern Panama.

Material cited as S. *dolichostylum* in Baker and Simmonds, *Flora of Trinidad and Tobago* (1953), is another taxon.

CANAL ZONE: Vicinity of Madden Dam, Chagres River, gravelly shore and bars at Landing, *Bartlett & Lasser 16778* (MO). COLÓN: Around Dos Bocas, Río Fató valley, 40–80 m, *Pittier 4204* (US, type of *Solanum imberbe* Bitt.). DARIÉN: Vicinity of Boca de Cupe, 40 m, growing in water along river edge, *Allen 905* (GH, MO, NY, US). Río Pirre, *Bristan 1482, 1483* (MO). El Real, Quebrada Trapiche, frequently found on banks of rivers, *Duke & Bristan 313* (MO, WIS). Gravel bar, Río Canasas, 100 m, *Duke 14511* (MO, WIS). 5 mi. SW of Pinogana on Río Tuira, common plant on sand and gravel bars, *Mori 365* (M, MO, WIS), *366* (MO, WIS). PANAMÁ: Along Pan American Highway, shrub by river, open grazed area near Jenine, *Duke 3844* (GH, MO, SCZ). Pan American Highway at Río Mamoni ca. 4 mi. beyond Chepo, shrub on sand bar, *Duke 5576* (MO). Chepo near river, flood plain weed, *Tyson 1428* (MO, SCZ). SAN BLAS: Near stream above Puerto Obaldía, *Gentry 1546* (MO).

47. **Solanum nudum** H. & B. *ex* Dun., Sol. Syn. 20. 1816. TYPE: *Bonpland s.n.* (P).

S. micranthum Willd. *ex* R. & S. *in* L., Syst. Veg. 4: 663. 1819. TYPE: Venezuela, *Humboldt s.n.* (B-W 4342, not seen; IDC 7440. 293. II. 8).

Bassovia foliosa Brandeg., Univ. California Pub. Bot. 6: 373. 1917. TYPE: Mexico, *Purpus 7565* (MO, NY).

Solanum parcebarbatum var. *minorfrons* Bitt., Fedde Repert. 18: 52. 1922. HOLOTYPE: *Cook & Griggs 146* (US).

Shrub or *tree* to 7 m tall; twigs and young branches greenish or yellowish, often slightly angled or longitudinally striate. *Leaves* 10–15 cm long and 3–5 cm wide, elliptical to lanceolate, mostly widest at or below the middle, acuminate at both ends, glabrate but whitish-pilose at the vein axils beneath and with a few hairs scattered on the lamina or near the veins; petioles 1–2 cm long; minor leaves ½ to almost as long as the majors and of similar shape and pubescence. *Inflorescences* mostly near the ends of the branches, subumbellate on a short, slender unbranched peduncle, the cicatrix mostly contracted and short; pedicels filiform, ca. 1 cm long in fruit elongating and thickening somewhat, not becoming stout and rigid but evenly thickening toward the apex. *Flowers* with the calyx truncate in bud with umbo-like lobes, usually splitting at the sutures when the corolla has emerged, bearing long, whitish, simple apical hairs, sometimes densely pilose but glabrous basally, in fruit glabrescent, not enlarged and the margins becoming irregular and misshapen; corolla white, often drying with a purplish hue, 5 mm long, lobed about ⅔ the way down; anthers ellipsoid, at least twice as long as broad, ca. 3 mm long. *Fruits* to 1.3 cm across, ripening ?yellow, mostly holding their shape in the press.

This species may be recognized in the field by its hairy leaf axils and globose fruits on slender pedicels. In dried material, the purplish hue of the corolla and the hairs on the calyx and leaf lamina are good distinguishing characters.

Solanum nudum ranges from Costa Rica and Guatemala to Argentina and Bolivia and is found in Venezuela and Trinidad. In Panama it is very frequent in roadside thickets and cafetals in the mountains of Chiriquí.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1,500–2,000 m, *Allen 1492* (GH, MO, NY, US). Between Bambito and Cerro Punta in weedy roadside area, *Croat 10548, 10573, 10626* (all MO). Between Río Chiriquí Viejo and Nueva California, pasture and roadside, *D'Arcy 4244* (MO). Roadside, Nueva California, *D'Arcy 4249* (MO). Plentiful in cafetal beside "Sonrisa Chiricana," Nueva Suisa, Volcán District, 5,700 ft, *D'Arcy 5313* (MO). Above Nueva Suisa, Volcán District, 6,000 ft, *D'Arcy 5325* (ADW, MO, MPU, PMA). At base of tree, Bambito, *D'Arcy 5339* (MO). Above Cerro Punta, 6,300 ft, *D'Arcy 5374* (MO). N side of Cerro Pando, 6,000 ft, in thicket, *D'Arcy 5402* (F, MO, WIS). Low weedy area N side of Cerro Pando, 6,000 ft, *D'Arcy 5406* (BIRM, F, MO). Above Boquete, 4,500 ft, *D'Arcy 5443* (ADW, F, G, MO, MPU). Bajo Chorro, Boquete District, rain forest, *Davidson 296* (A, MO, US). Valley of the Río Chiriquí Viejo N of Volcán City, 5,200–5,600 ft, *Duke 9011* (WIS), *9012* (MO). Cerro Horqueta, 1,500 m, *Duke et al. 13690* (MO, SCZ). Road between Boquete and Cerro Horqueta, *Duke 13720* (C, MO, SCZ). NW of Boquete, Cerro Horqueta, 5,000–5,800 ft, trail to lower edge of cloud forest, *Dwyer et al. 489, 555* (both MO). Boquete, 5,000 ft, *Dwyer 6969* (MO). Roadway near Hotel Dos Río, Boquete, *Dwyer 7638* (MO). Cerro Horqueta, rain forest, 4,500–5,500 ft, *Dwyer & Lallathin 8759* (MO, UCWI). Vicinity of El Boquete, foot of Sierra spur, abandoned lands, "Ajucillo," *Maurice 706* (US). Upper Río Chiriquí Viejo, vicinity of Monte, growing on hillsides, 1,300–1,900 m, *Seibert 167* (MO). Cerro Punta, 6,025 ft, *White 197* (GH, MO). Vicinity of Callejón Seco, Volcán de Chiriquí, 1,700 m, *Woodson & Schery 487* (GH, MO, US). PANAMÁ: Río Tapía, moist forest, *Standley 28206* (US).

48. **Solanum rovirosanum** Donn. Sm., Bot. Gaz. (Crawfordsville) 48: 297. 1909. TYPE: Guatemala, *Türckheim 11021* (= Donn. Sm., *Pl. Guat. 8716*) (US).

S. *confertiseriatum* Bitt., Fedde Repert. 11: 490. 1912. SYNTYPE: Ecuador, *Eggers 14219* (MO).

Cyphomandra homalophylla Standl., Trop. Woods 10: 50–51. 1927. TYPE: Panama, *Cooper & Slater 39* (F, US).

Solanum grandifolium Mort., Contr. U. S. Natl. Herb. 29: 51–52. 1944. HOLOTYPE: Colombia, *Cuatrecasas 7394* (US).

Shrub or small *tree* to 7 m tall; twigs stout, glabrous or minutely puberulent. *Leaves* large, ovate or elliptic, to 30 cm long, narrowed at each end, glabrous above, beneath glabrous or minutely puberulent, the midvein prominent; petiole stout, 1–5 cm long; minor leaves not evident. *Inflorescence* terminal or axillary, a once or twice branched cyme of secund, elongating, flexuous racemes which bear conspicuous pedicel scars, the pedicels filiform, 6–9 mm long, becoming thicker and slightly longer in fruit. *Flowers* small, the calyx 1–2 mm long, campanulate, splitting about halfway down into mucronulate lobes, glabrous and mostly drying russet; corolla white, drying orange-brown, ca. 6 mm long, deeply lobed, the lobes lanceolate; filaments united into a tube ca. 1 mm long, glabrous, each filament flattened but not narrowed apically, adnate to the full breadth of the anther base, but not extended over the dorsal surface of the anther, the anthers stout, dorsally flattened, 3–4 mm long, opening by large terminal pores which are tardily confluent with longitudinal slits; ovary elliptical with a few small hairs on top, the style pubescent, the stigma placed 1.5 mm beyond the anther tips. *Fruit* globose, to 10 mm across (immature), flattening in the press.

This species is similar to some species of *Cyphomandra* in its long peduncles. It is distinguished by its large leaves, pubescence not usually visible to the naked eye and its elongate, branched inflorescences.

In Panama, *Solanum rovirosanum* has been collected only in the lowlands of Bocas del Toro, although it ranges widely from Guatemala to Colombia and Ecuador.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 39, 118* (F). Río Teribe just below Puerto Palenque, 250 ft, *Kirkbride & Duke* 555 (C, MO, SCZ). Down Changuinola River from town of Changuinola, ½ mi. from point of entry into the sea in a vast bare floodplain, *Lazor et al. 2639* (FSU, SCZ). Along Changuinola River ½ mi. from point of entry into the sea, *Lazor et al. 2657* (FSU, SCZ). 4 mi. N of Almirante, lower montane rain-forest, *McDaniel 5097* (MO). Water Valley, *von Wedel 731* (MO, US). Vicinity of Chiriquí Lagoon, *von Wedel 1085* (GH, MO, US).

Subgenus **Potatoe** (G. Don) D'Arcy, Ann. Missouri Bot. Gard. 59: 272. 1972 [1973].

Subsect. *Potatoe* G. Don, Gen. Syst. 4: 400. 1838. TYPE: S. *tuberosum* L.

Herbs or *vines*, rarely woody, often glandular-pubescent and aromatic, unarmed, hairs unbranched (simple). *Leaves* mostly compound or deeply lobed, with simple, entire leaves often present at some stage. *Inflorescence* mostly paniculate, the peduncles once- or ternately-branched, often pendulous; pedicels mostly articulating near the base or above it. *Flowers* small to medium-sized, often showy, calyx not much accrescent, truncate to deeply lobed; corollas shallowly lobed with a united plicae region; anthers mostly stout and little-tapered, opening introrsely by large terminal pores; ovary glabrate. *Fruit* mostly a juicy berry, globose or ellipsoid and the apex conical; seeds compressed.

Several lianous sections of the genus display a similarity of inflorescence and pubescence types and are here united into one subgenus. In many species, the pedicels are described as articulating at the base, but this is not strictly so, for there is usually a short portion of pedicel remaining on the peduncle as an elevated pedicel scar. If this articulation, often slightly enlarged, is the locus of an ancestral bract or bracteole, then the inflorescence may be a fundamentally different structure from that in other subgenera.

In Panama, subgenus *Potatoe* is represented by sections *Petota*, *Basarthrum*, *Anarrhichomenon* and *Jasminosolanum*. Section *Aculeigerum* may also belong here instead of in subgenus *Leptostemonum*.

P. Section **Petota** Dumort., Fl. Belg. 38. 1827. TYPE: S. *tuberosum* L.

Sect. *Tuberarium* (Dun.) Bitt., Fedde Repert. 11: 349. 1912. TYPE: S. *tuberosum* L.

Unarmed *herbs*, *vines* or *shrubs*, often glandular-pubescent with simple hairs, aromatic, often tuber-bearing. *Leaves* mostly odd-pinnate with interstitial leaflets. *Inflorescence* an open panicle or raceme, pseudoterminal becoming lateral, the peduncles usually leafy towards the base; pedicels articulating well above the base. *Flowers* small to medium-sized; anthers elongate or elliptical, tapering slightly, opening by large introrse terminal pores and ultimately longitudinally. *Fruit* globose, ovate or elliptical, pendant or not.

Species of this section occur from Wyoming on the north to south of the Chiloé Archipelago in southern Chile. They are mostly plants of upland areas, and of the 157 species recognized by Correll (1962), only 14 are reported below 1,000 m and about two dozen below 2,000 m. The majority of species ranges between 2,000 and 4,000 m, but some grow at higher elevations. In Panama all collections are from the Chiriquí mountains.

Useful references:

Correll, D. S. The Potato and its Wild Relatives. Renner, Texas. 1962.

Hawkes, J. G. A revision of the tuber-bearing *Solanums*. Scott. Pl. Breed. Sta. Rec. 1963: 76–181.

a. Fruits globose; plants coarsely pubescent; pedicels articulating at or well above the middle; terminal leaflet usually much larger than the others; anthers often tapering at the apex; cultivated species ..... 50. *S. tuberosum*

aa. Fruits ellipsoid or conical; stems glabrate, leaves often pubescent but not coarsely so; pedicels articulating at or well below the middle; terminal leaflet usually only slightly larger than the others; anthers elongate or elliptical but not tapering at the apex; native species occurring in the wild.

b. Small dense plants; leaflets broadly elliptical, obtuse apically, reticulate-veined beneath; calyx 3 mm long, the lobes broadly deltoid ..... 51. *S. woodsonii*

bb. Ascending plants of open habit; leaflets elliptical, not usually broadly so, acuminate apically, minor venation obscure beneath; calyx 5 mm long, the lobes lanceolate ..... 49. *S. oxycarpum*

49. **Solanum oxycarpum** Schiede *in* Schlecht., Hort. Halensis 1: 5, *tab.* 3. 1841. TYPE: Mexico, *Schiede s.n.* (HAL, not seen).

Ascending or low and spreading perennial *herb*, sarmentose and tuber-bearing; stems glabrescent. *Leaves* 3–12-foliolate, leaflets to 3.5 cm broad and 6 cm long but mostly about half that size, the terminal leaflet largest and the basal pair reduced, ovate, mostly acute apically, basally obtuse or rounded, sometimes oblique, glabrate beneath, above with short, scattered hairs; interstitial leaflets few, small; petioles mostly 2–4 mm long; minor leaves sometimes wanting. *Inflorescence* axillary or appearing terminal, standing above the leaves, a few-flowered panicle; the peduncle glabrous, sparingly branched, 5 cm long; pedicels 1.5–2.5 cm long, erect, glabrate, filiform, articulated at about the middle or below. *Flowers* medium-sized; calyx 5 mm long, relatively broad, glabrate, lobed to about ⅓ the way down, the lobes lanceolate; corolla lavender, rotate, ca. 3 cm across, lobed to ⅕ the way down; anthers elongoid, 3–4 mm long. *Fruit* (Correll) 2–3 cm long, ovoid to cylindric, green.

This species is superficially similar to *S. caripense* Dun., but differs in its larger purplish flowers as well as the pedicel articulation at or near the middle. It ranges from southern Mexico to Chiriquí Province, mostly in humid forests at middle elevations. Prof. J. G. Hawkes, University of Birmingham, has stated (personal communication) that the single collection known from Panama is somewhat anomalous when considered against the bulk of Central American material and that further examination may suggest recognition of a distinct species.

CHIRIQUÍ: Bajo Choro, rain forest, 1830 m, *Davidson 314* (F, cited by Correll 1962: 188).

50. **Solanum tuberosum** L., Sp. Pl. 185. 1753. LECTOTYPE: Herb. Linn. 248.12 (LINN; microfiche LINN 138: II. 4).

No herbarium specimens of this species have been seen from Panama. The distinguishing features of the species are presented in the key.

A considerable acreage is devoted to this crop in the Volcán district of Chiriquí Province. In addition to the cultivated plants, occasional spontaneous individuals are to be found around sheds and by paths in this district, but it is not known whether they grow to flowering or fruiting maturity.

The tubers are an important food starch in most parts of Panama. "Irish potatoes" (English), "papas" (Spanish).

51. **Solanum woodsonii** Corr., Wrightia 2: 137. 1961. TYPE: Panama, *Woodson & Schery 399* (GH, MO, US).

Low spreading perennial *herb*, less than 20 cm above the ground, sarmentose and tuber-bearing; stems puberulent. *Leaves* mostly 5-foliolate, leaflets 2 cm broad and 3.5 cm long, the terminal leaflet slightly larger, broadly elliptical, obtuse apically, basally rounded, slightly oblique, with conspicuous coarse glandular hairs above, finely puberulent and reticulate-veined beneath; petioles less than 5 mm long, often almost absent; minor leaves wanting. *Inflorescence* almost terminal, standing above the leaves, the peduncle 5 cm long, slender, sparingly branched, puberulent to hispid; pedicels filiform, 1.5–2 cm long, erect, dark, finely hispid, articulated variously near the middle to ⅓ the way down. *Flowers* with the calyx 3 mm long, relatively broad, lobed to ⅓ the way down, the lobes broadly deltoid; corolla pale purple, ca. 3 cm across, rotate, lobed to ⅕ the way down; anthers stout, 3–4 mm long.

This species is known only from three collections, one from Venezuela. On technical characters it is very like S. *oxycarpum* Schiede, but Correll mentions a tendency to lobing on the dorsal side of the anthers. In general appearance, the type collection of S. *woodsonii* is quite different from any specimens seen of S. *oxycarpum* in having much broader, more rotund leaflets and a much denser aspect.

CHIRIQUÍ: Potrero Muleto, Volcán de Chiriquí, 3,150 m, *Davidson 1017* (F, cited by Correll 1962: 203). Potrero Muleto to summit, Volcán de Chiriquí, 3,500–4,000 m, flowers pale purple, *Woodson & Schery 399* (GH, MO, US).

Q. Section **Basarthrum** (Bitt.) Bitt., Bot. Jahrb. Syst. 54: 499. 1917.

Subsect. *Basarthrum* Bitt., Fedde Repert. 11: 350. 1912. LECTOTYPE: S. *suaveolens* Kunth & Bouche.

Perennial *herbs*, scandent *shrubs* or *lianas*, hairs often 2-celled "bayonet hairs," the basal cell conspicuously larger, mostly not glandular-pubescent, non-tuber-bearing. *Leaves* odd-pinnate usually with interstitial leaflets. *Inflorescences* mostly open-paniculate, pseudoterminal on branches or short shoots, often becoming axillary or lateral, elongating in fruit; pedicels articulating just above the base and usually leaving an elevated pedicel scar. *Flowers* small to medium-

sized; stamens equal, the anthers elongate or elliptical, not much tapered, opening by large introrse terminal pores and also longitudinally. *Fruit* ellipsoid to ovoid, rarely globose, sometimes large, pendant.

Species of this section occur from Mexico to northern Chile. Characteristic of upland regions of the American tropics, they do not range into regions where there is seasonal frost.

Correll (1962) divided this section into six series, one of which is here removed to sect. *Anarrhichomenum*. The two Panamanian species were placed in different series, apparently closely related. Two of the remaining series of sect. *Basarthrum* from South America, series *Muricata* and series *Articulata*, may belong in this alliance. The group has been considered a subsection of sect. *Petota* by many workers, the main unifying feature being the presence of interstitial leaflets on the pinnate leaves, a character not unique to sect. *Petota* but also occasionally occurring in section *Jasminosolanum*.

Useful reference:
Correll, D. S. The Potato and its Wild Relatives. Renner, Texas. 1962.

a. Leaves and peduncles glabrate, the pedicels glabrous; leaflets mostly more than 7, about 3 times as long as broad ..... 52. *S. canense*
aa. Leaves hispid or sericeous, amply pubescent, the peduncles and pedicels with prominent spreading hairs; leaflets fewer than 7, usually 3, these about twice as long as broad ..... 53. *S. caripense*

52. **Solanum canense** Rydb., Bull. Torrey Bot. Club 51: 174. 1924. TYPE: Panama, Darién, Cana, *Williams 844* (NY).

Scandent perennial *herb* or *vine* festooning in thickets and perhaps high climbing; stems slender, angled, glabrate. *Leaves* 9–15-foliolate, mostly with small, rotund interstitial leaflets, the rachis arching backwards, leaflets to 6 cm long and 1–2 cm broad, narrowly elliptical or lanceolate, apically acute, basally rounded, often oblique, glabrate or with scattered small hairs on the lamina and the midveins puberulent; petiole often bearing interstitial leaflets to the base, the petiolules to 1 cm long or almost wanting. *Inflorescence* lateral, a few-flowered raceme 4–6 cm long; pedicels filiform, 5–8 mm long, elongating and thickening somewhat in fruit, articulating near the base, glabrous. *Flowers* small, calyx less than 1.5 mm long, subtruncate with dark, umbonate teeth; corolla white with a dark eye, 1–1.5 cm across, lobed to about the middle; filaments very short. *Fruit* globose to ellipsoid, 1.5–2 cm long, green and striped.

This species is recognized by its scandent habit, small white flowers which individually resemble those of sect. *Solanum*, and by the many narrow leaflets.

Solanum canense occurs at low to middle elevations from southern Guatemala to Ecuador and western Venezuela.

COCLÉ: Hills NE of El Valle de Antón, 2,000 ft, disturbed forest edges, *Lewis et al. 1805* (MO). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, *Porter et al. 4595* (MO) rain forest. DARIÉN: Río Tuira 2 mi. upstream from Boca del Cupe, in open field, flowers white, *Duke 5379* (MO). PANAMÁ: Cerro Campana, *Allen 2087* (MO, NY, US). Forest near dam site of Cañita, *Croat 14506* (SCZ). Dam ca. 5 mi. S of Cañita, in mature forest above Bayano River, *D'Arcy 5188* (ADW, BIRM, C, F, MO, PMA, UCWI).

FIGURE 28. *Solanum caripense* Dun., habit (× ½). [After *D'Arcy 6434* (MO).]

53. **Solanum caripense** H. & B. *ex* Dun., Sol. Syn. 8. 1816. TYPE: Venezuela, *Bonpland s.n.* (P; microfiche 6209. 60: II. 2).—FIG. 28.

Herb or *vine* to 2 m long, climbing in thickets and trees; stem branched; twigs pilose-hirsute, the hairs when dried with a yellowish cast. *Leaves* mostly 3-foliolate, occasionally entire or to 7-foliolate; leaflets to 7 cm long and 4 cm broad, the terminal leaflet usually larger and the leaflets proximal to the terminal 3 often much reduced, broadly elliptical to lanceolate, acuminate apically, mostly rounded basally, hispid or sericeous on both sides, reticulate-veined beneath; petioles and petiolules hispid, the former to 6 cm long; minor leaves prominent, rotund. *Inflorescence* a several-flowered, open raceme or rarely a panicle,

pseudoterminal becoming lateral, the peduncle to 5 cm long, slender, in fruit elongating and pendant; pedicels filiform, to 15 mm long, dark-colored, sparingly hispid, articulating just above the base. *Flowers* inconspicuous, calyx 4–5 mm long, purplish, lobed more than halfway down, the lobes lanceolate, some sometimes larger than the others; corolla white, 1–2 cm across; filaments basally connate, the anthers 3–4 mm long. *Fruit* ellipsoid to ovoid, 3 cm long, green with dark stripes.

This species is usually recognizable by its climbing habit, mostly trifoliolate leaves, and overall pubescence. For distinctions between related species in neighboring countries see Correll (1962).

Solanum caripense ranges from Costa Rica to Peru and Venezuela, occurring at the edges of thickets or woods. In Panama it has been collected only at middle and upper elevations in Chiriquí Province.

CHIRIQUÍ: Finca Collins, vicinity of Boquete, *Blum & Dwyer 2588* (MO, SCZ). Above Cerro Punta, 7,600 ft, climbing in tree, *D'Arcy 5354* (MO). South side of Cerro Pando, 6,000 ft, abandoned cultivation, *D'Arcy 5391* (MO). Edge of pasture above Boquete, 5,200 ft, *D'Arcy 5459* (MO). NW of Boquete, Cerro Horqueta, 5,000–5,800 ft, trail to lower edge of cloud forest, *Dwyer et al. 452* (MO). Río Chiriquí Viejo valley near Monte Lirio, *White 68* (MO; cited as *S. fraxinifolium* var. *protoxanthum* (Bitt.) Bitt. by Correll, 1962: 94). Between Boquete and La Popa, *D'Arcy & D'Arcy 6434* (MO).

R. Section **Anarrhichomenum** Bitt., Fedde Repert. 11: 247–249. 1912. TYPE: *S. sodiroi* Bitt.

Unarmed, root-climbing *vines* or *shrubs*, epiphytic or sometimes trailing on rocks or ground, with simple hairs or sometimes branched hairs on young parts. *Leaves* simple or compound, the leaflets entire, small, short-petioled, often coriaceous, interstitial leaflets wanting but minute minor leaves often present. *Inflorescence* terminal on branches or on mostly leafy short shoots, a small, several-flowered panicle or simple raceme, sometimes consisting only of solitary or paired flowers; pedicels articulating at the base, sometimes leaving a prominent cicatrix. *Flowers* mostly small; calyx often succulent; corolla white, blue, purple or pink, lobed more than halfway; stamens equal, oblongoid or elliptical, not much tapering, dehiscing by large terminal pores which may extend to the base of the theca; style often pubescent, exserted or included. *Fruit* globose or ellipsoid-conical, red, orange or purplish to black, the stylar scar often conspicuous.

This section is best recognized by the adventitious roots, the entire or sparingly divided leaves, the small minor leaves, and the pointed fruits which are deciduous at the base of the pedicel.

Relationships of this group of species are poorly understood, and there is little agreement among botanists as to the correct placement. The usual presence at some stage of minor leaves argues for a recaulescent branching pattern and suggests correct placement in subgenus *Potatoe*. "Bayonet hairs," usual to species of sect. *Basarthrum*, are absent, as are interstitial leaflets.

The section includes about a dozen species ranging from Mexico to Peru with only slight extension into ultramontane South America.

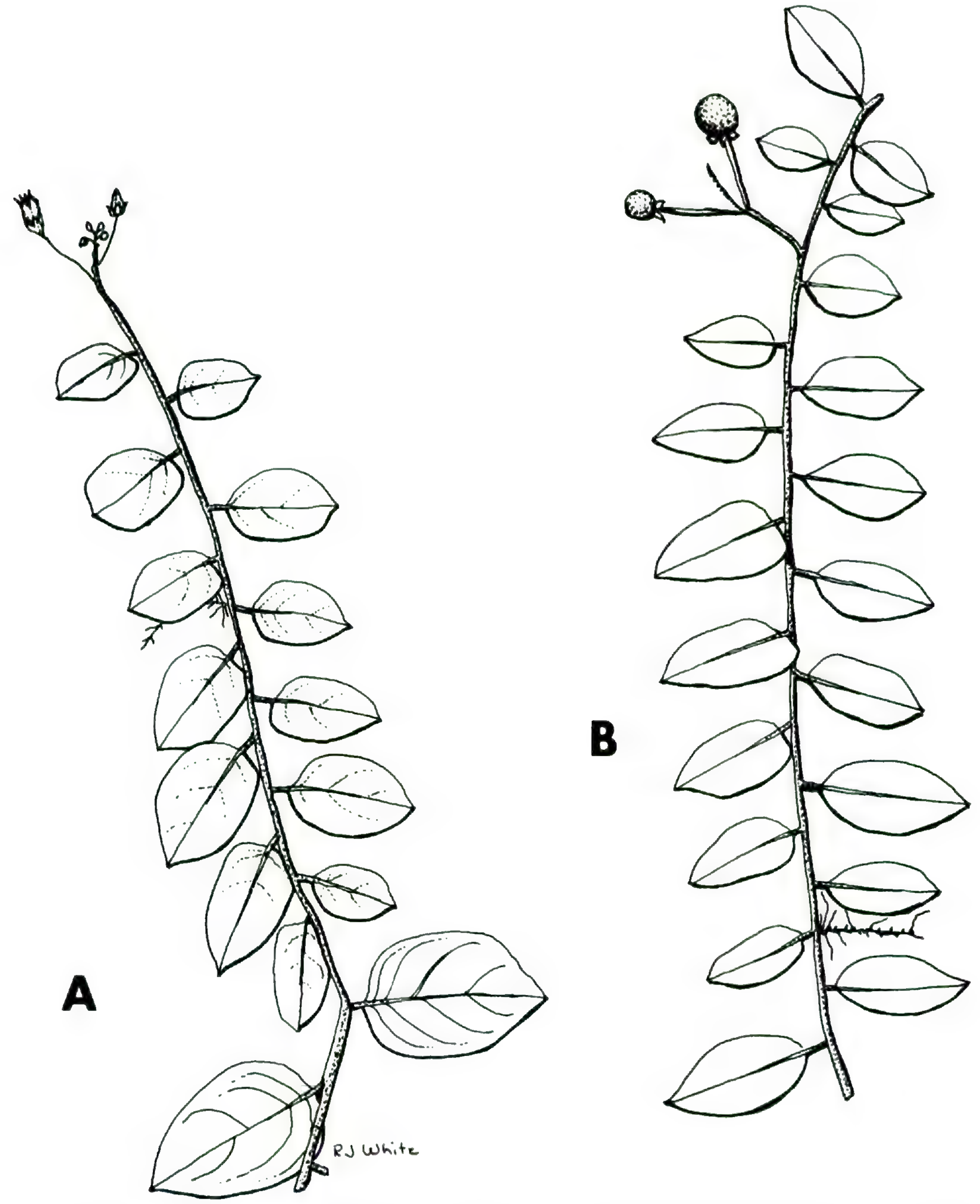

FIGURE 29. *Solanum evolvulifolium* Greenm.—A. Habit in flower (× ¾). [After *Woodson & Schery 649* (MO).]—B. Habit in fruit (× ¾). [After *Allen 4995* (MO).]

54. **Solanum evolvulifolium** Greenm., Bot. Gaz. (Crawfordsville) 37: 211. 1904. TYPE: Costa Rica, *Tonduz* [non Pittier] *7413 ex* Donn. Sm., *Pl. Guat.* (GH, K, NY, US).—FIG. 29.

?S. *loxophyllum* Bitt., Fedde Repert. 11: 14. 1912. TYPE: Ecuador, *Sodiro 114/20* (?B, not seen; MO, photo).

Epiphytic *shrub* or *vine*; branches 30–35 cm long, slender, pilose, rooting at the nodes. *Leaves* 3 cm long, distichous, rhombic-ovate, somewhat oblique,

gradually diminishing in size to the apex of the branch, entire or slightly repand, basally rounded, truncate or sub-cordate, above densely pilose on the midvein, glabrate on the lamina, the lateral venation obscure, beneath glabrous; petioles diminishing from 5 mm to 1.5 mm long near the apex of the branch, pilose; minor leaves minute, 1–2 mm long, caducous. *Inflorescence* terminal on leafy branches or on nearly leafless, short, axillary spurs, several- to many-flowered, an open pendulous panicle or short raceme, the peduncle an extension of the twig, pilose with conspicuous pedicel scars; pedicels filiform, thickening and becoming turbinate in fruit, glabrate, 1.5–2 cm long. *Flowers* small, calyx 2 mm long, in bud craterform with acerose teeth, becoming lobed ⅓ the way down, the lobes rotund-mucronate, glabrous; corolla pink, rotate, ca. 8 mm across, lobed to near the base, the lobes narrow, acuminate, in bud forming a pointed apex; anthers 3 mm long, opening by very large terminal pores which continue to the base of the thecae; ovary glabrous (Greenman). *Fruit* sub-globose, slightly apiculate, 8 mm across; seeds 2.5 mm long (Greenman).

Solanum evolvulifolium is distinctive in the Panamanian solanaceous flora in its distichous, root-climbing epiphytic habit, apparently clinging to the bark of trees in the manner of species of *Marcgravia*, *Philodendron*, or *Peperomia*. The inflorescences are quite variable in size, only the larger ones presenting long pendulous fruits.

Greenman suggested that this species does not differ from S. *boerhaavifolium* Sendt. of Brazil. However, the petioles of that species are much longer, the flowers much larger and there are no minute, early deciduous minor leaves. Bitter in describing S. *loxophyllum* (of which he had no flowers) suggested it might form a new section *Loxophylla* in its own right. *Solanum evolvulifolium* bears a close resemblance to S. *holophyllum* Bitt., and, but for the entire leaves, to S. *sodiroi* Bitt. The pink or flesh-colored flowers are unusual in the genus.

Solanum evolvulifolium ranges from Costa Rica to Colombia and, if the synonymy of S. *loxophyllum* is accepted, to Ecuador.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, 6,000–7,000 ft, epiphytic herb, *Allen 4995* (G, MO). CHIRIQUÍ: Bajo Chorro, Boquete district, rain forest, epiphytic vine, 6,000 ft, *Davidson 112* (A, MO, US). Vicinity of Bajo Chorro, 1,900 m, epiphyte, *Woodson & Schery 649* (MO, US).

S. Section **Jasminosolanum** Bitt. *ex* Seithe, Bot. Jahrb. Syst. 81: 291. 1962. TYPE: S. *jasminoides* Paxt.

Unarmed *herbs* or *lianas*, glabrate with simple or sparingly branched hairs; stem slender. *Leaves* simple or compound, entire or lobed, often all on the same plant; interstitial leaflets sometimes present; minor leaves present or not, usually of different appearance from the majors. *Inflorescence* terminal or lateral, ebracteate, a many-flowered, open, pendant or erect panicle; the pedicels articulating at or almost at the base. *Flowers* often showy, calyx small, truncate, in some species with enlargement in the lower portion, only slightly accrescent; corolla small or large, white or variously colored, variously lobed; stamens equal, anthers stout or elongate but not much tapering, opening by large, slightly

introrse terminal pores and ultimately longitudinally; ovary glabrous. *Fruit* a juicy, globose berry.

This section comprises a few species of Central and South America, some of them widely cultivated for ornament. Plants in Panamá are probably introduced. The section is recognizable by the showy pendulous panicles of flowers and globose fruits. It differs from sect. *Petota* in its woodiness and in the low articulation points on the pedicels, and it differs from sect. *Basarthrum* in its usually globose fruits and in the absence of bayonet hairs.

55. **Solanum seaforthianum** Andr., Bot. Rep. 8: *tab. 504.* 1808. TYPE: (not seen).—FIG. 30.

High climbing *liana*, glabrous, the stems slender, green, becoming woody. *Leaves* simple, compound or lobed, often all on the same plant, the lobes mostly ovate, the sinuses broadly rounded, apically long-acuminate, basally acute, obtuse, truncate or cordate; petioles 3–5 cm long. *Inflorescence* a large, showy, ternately-branching panicle, the peduncle slender; pedicels slender and abscissing nearly at the base; calyx 2–3 mm long, apically truncate or with very short deltoid or umbonate lobes, not splitting at the sinuses and not expanded in the lower portion; corolla purple, pinkish, blue or rarely white, 2–5 cm across, lobed to more than one half the way down; stamens subequal, the filaments glabrous, short, the anthers stout, 2.5–3.5 mm long, dehiscing by large terminal pores which may coalesce, and ultimately by longitudinal slits; ovary and style glabrous, the stigma small, capitate. *Fruits* globose, 1–2 cm across, bright, shiny, deep scarlet, juicy; seeds 3.5 mm across.

This species is a native of the West Indies but is widely cultivated for ornament in tropical gardens and is naturalized in a number of parts of the world, including Panama.

CANAL ZONE: Near beach at Ft. Kobbe, *Duke 4199* (MO). Farfan Beach, *Dwyer 6785* (MO). Farfan Beach Road, *Kirkbride & Elias 62* (MO, NY). Fort Amador or causeway and islands, *Tyson 2011, 2028* (both MO, PMA). CHIRIQUÍ: Vicinity of Finca Lérida, 1,750 m, *Woodson & Schery 239* (GH, MO, US). LOS SANTOS: Los Asientos, *Wendehake 26* (DUKE, MO), *29* (MO, PMA). PANAMÁ: Cerro Chame, 25 m, *Allen 2243* (MO). Nueva Gorgona, sea level, *Allen 3764* (MO).

T. Unnamed Section.

56. **Solanum granelianum** D'Arcy.[43] TYPE: Panama, *Terry & Terry 1605* (MO, holotype; A, MO, isotypes).

Woody *vine*, twigs stout, minutely puberulent with erect, curving, simple hairs. *Leaves* ovate, to 12 cm long, apically short acuminate, basally rounded or obtuse, glabrous, the margins entire, veins 2–4 on each side of the midvein;

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[43] *Solanum granelianum* D'Arcy, spec. nov. Labrusca lignescens, ramunculis crassis, minute pilosis; foliis glabris, ovatis; inflorescentia terminalibus, paniculatis, multifloridis, pedicellis supra glabratis infra dense puberulentibus; calyce 2–3 mm longo, glabrato, apice truncato, basim umbonis parvis gerentibus; corolla ad basim lobata, dense minute pubescentia, imo glabra; antheris an aequalibus, nigrescentibus rimis pororum apicalium in sicco luteis.

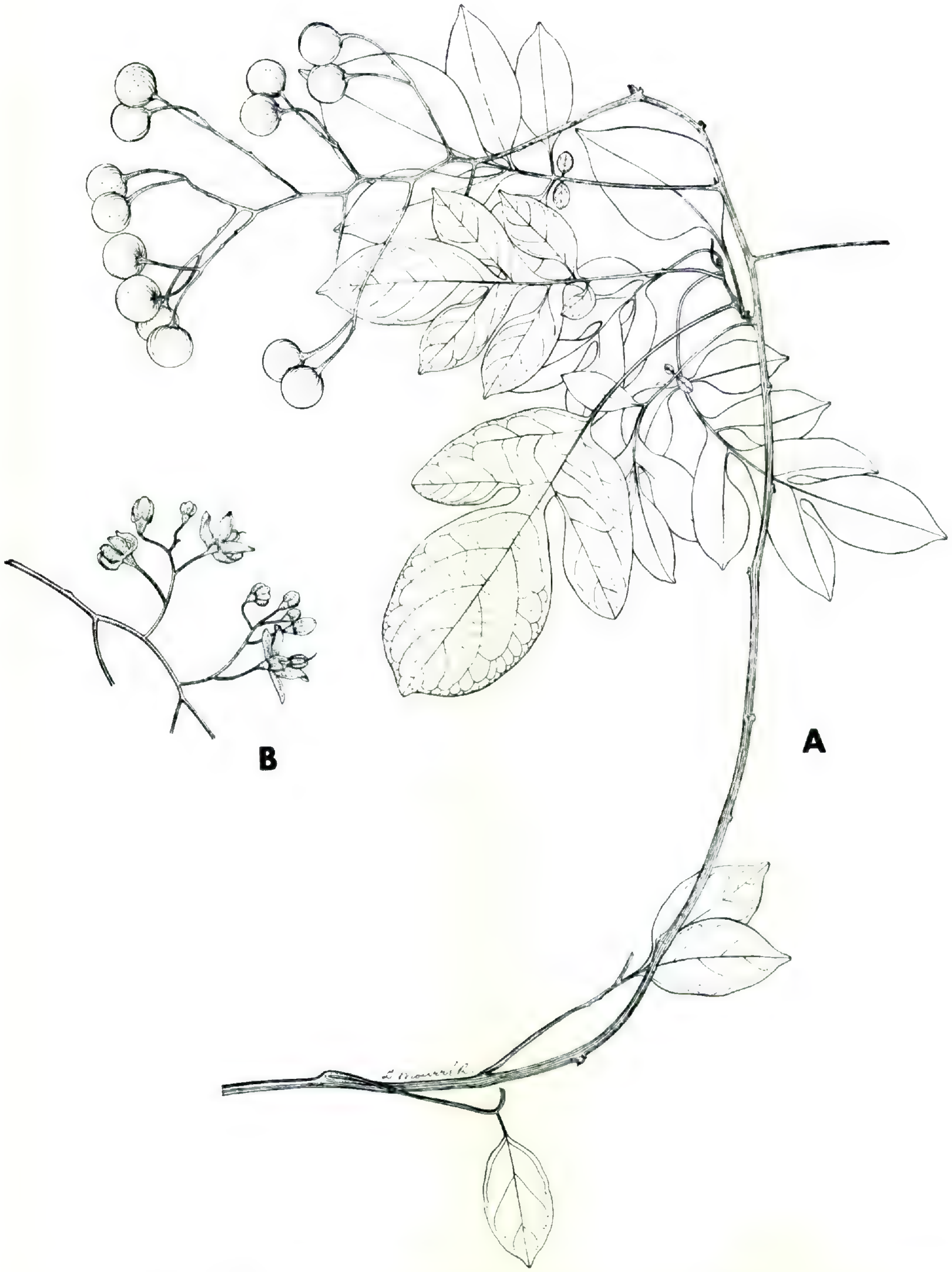

FIGURE 30. *Solanum seaforthianum* Andr.—A. Fruiting branch (× ⅗). [After *Wendehake 29* (MO).]—B. Portion of flowering panicle (× ⅜). [After *Tyson 2028* (MO).]

petioles 1.5–2.5 cm long, glabrous or with some minute erect hairs. *Inflorescence* an open, terminal, many-flowered panicle, the peduncles stout, mostly glabrous, the ultimate divisions minutely puberulent with a conspicuous, open, irregularly spaced cicatrix of pedicel scars; pedicels slender, 9–15 mm long, apically glabrate,

puberulent toward the base. *Flowers* with the calyx craterform, 2–3 mm long, apically truncate, with several inconspicuous swellings in the lower portion; the corolla ca. 11 mm long, lobed nearly to the base, densely fine pubescent outside except for the basal area, the lobes lanceolate; the stamens probably equal, anthers ca. 6 mm long, drying dark with contrasting light colored rims around the apical pores; style ca. 5 mm long, apically geniculate, densely puberulent overall. *Fruit* not seen.

This species is distinctive in its fine pubescence of minute erect hairs and in the densely pubescent corolla and style. The calyx resembles that of *S. surinamense* Steud., but the anthers are quite different in that species. From the limited material at hand it is not feasible to ascertain what the stamens are like. It may not be correctly placed in this genus.

It takes its name from M. Granel de Solignac, a descendant of M. F. Dunal and an invaluable aid to visitors to Dunal's material at the Institut Botanique, Montpellier.

DARIÉN: Rain forest, crest of Cana-Cuasi Trail, Chepigana District, woody vine, flower blue, *Terry & Terry 1605* (A, F, MO).

21. WITHERINGIA

Witheringia L'Heritier, Sert. Angl. 33, *tab. 1.* 1788. TYPE: *W. solanacea* L'Her.

Sicklera Sendt., Flora 29(13): 179, error, for 195. 1846. TYPE: *S. solanacea* Sendt.
Brachistus Miers, Ann. Mag. Nat. Hist., Ser. 2. 3(16): 262. 1849. TYPE: *Witheringia stramoniifolia* Kunth *in* H. & B.
?*Fregirardia* Dun. *ex* Delile, Ind. Sem. Hort. Monsp. 3, 7. 1849, fide Index Nominum Genericorum.
Vassobia Rusby, Bull. New York Bot. Gard. 4: 422. 1922. TYPE: *V. atropoides* Rusby (= *Witheringia dichotoma* (Rusby) D'Arcy).
Bassovia sensu auct., non Aubl., Hist. Pl. Guiane Fr. 1: 217, 3: *tab.* 85. 1775.

Unarmed, erect *herbs* or *subshrubs* with simple or dendritic hairs; stems often fistulose. *Leaves* simple, entire or sinuate dentate, membranaceous, mostly petiolate; minor leaves mostly present and smaller than the major leaves. *Inflorescence* axillary, mostly a condensed, many-flowered raceme, or by obsolescence of the peduncle a fascicle, rarely paniculate, solitary or few-flowered; pedicels slender, often holding the flowers beneath the leaves and recurving to hold the fruits above them. *Flowers* 4–5(–6)-merous, mostly small, the calyx cyathiform, the apex truncate or with umbos or teeth, sometimes splitting with age; the corolla mostly rotate, salverform to tubular-campanulate, the relative length of the tube variable, glabrous or puberulent outside, inside mostly with a ring of pubescence at the level of stamen insertion; stamens equal or nearly so, filaments mostly inserted at or above the middle of the corolla tube, mostly pubescent, the anthers yellow or purple, ovoid or oblong, the connective in most species prolonged into a small apicule; ovary glabrous or pubescent, 2-loculed, the placenta proliferated, ovules many. *Fruit* a juicy, many-seeded berry, mostly bright colored, glabrous or pubescent, sometimes partly enveloped by the accrescent calyx; seeds compressed-discoid or fabiform, the surface with a crystalloid reticulate covering over the edges and in some species over all sides.

Plants of this genus have long been erroneously placed under a number of other genera, *e.g. Athenaea*, *Bassovia*, *Capsicum*, *Lycianthes*, *Saracha*, and *Solanum*, and only recently was their unity clarified by Hunziker (1969). The anthers, with longitudinal dehiscence and in many species with an extension of the connective into an apicule, the mostly tomentose filaments inserted in the upper portion of the narrow corolla tube, and the 5-ribbed calyces are good distinguishing features. In the field, the usually fascicled flowers held below the leaves and the bright, juicy fruits held above the leaves are useful characters for recognition.

Although Hunziker (1969) provided a synopsis of *Witheringia*, and both Sleumer (Lilloa 23: 117. 1950) and Hunziker (Bol. Acad. Nac. Ci. Córdoba 41: 211. 1960) discussed *Dunalia* and *Acnistus*, a clarification of distinctions between *Witheringia* and *Acnistus* is yet to appear. In *Acnistus arborescens* (L.) Schlecht.,[44] the type species of *Acnistus*, the flowers are fascicled, the anthers are apiculate and longitudinally dehiscent, the corolla shape and filament insertion resemble species of *Witheringia*, and on its seeds there is a good suggestion of the transparent reticulum present on seeds of *Witheringia*. In general, species of *Acnistus* and *Dunalia* have pubescence of a characteristic appearance and topography, and the calyces are of a different texture than those in *Witheringia*. Most species have much larger corollas with relatively longer tubes and shorter lobes than in *A. arborescens*. *Discopodium*, a small genus of central Africa, may be congeneric with *Witheringia* or *Acnistus*. A comparative study of these groups is desirable. The name *Witheringia* dates from 1788, *Acnistus* Schott. from 1831, *Dunalia* H.B.K. from 1818, and *Discopodium* Hochst. from 1844. *Dunalia* Schott. is conserved over *Dunalia* Spreng., 1815, Rubiaceae.

Hunziker (1969) reduced the genus *Brachistus* to rank of section under *Witheringia*, and this decision is followed here with reservation. *Witheringia stramoniifolia*, the type species of the section, has valvate calyx prefloration compared with complete prefloration in species of sect. *Witheringia*.

As now constituted, *Witheringia* comprises about 18 species ranging from Mexico to northern South America and perhaps one species in the South Seas. Twelve species, mostly of sect. *Witheringia*, occur in the Colombia to Costa Rica confine, and 8 of these are endemic. Section *Brachistus* occurs mainly from Mexico to British Honduras, but *W. stramoniifolia* is known from Panama.

The genus takes its name from William Withering, 1741–1838, an English physician and botanist.

Useful reference:

Hunziker, A. T. Estudios sobre Solanaceae 5. Kurtziana 5: 101–179. 1969.

a. Calyx with terminal teeth or lobes evident in bud and later stages; calyx accrescent in fruit.
b. Pubescence of simple or glandular hairs, dendritic hairs if present not frequent.

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[44] For unknown reasons, *Acnistus arborescens*, which ranges from Mexico to Brazil and throughout the Antilles, has not been found in Panama. In the countries where it occurs, it is common as a shrub of roadsides and successional forests. The filaments are glabrous and the nodes of the inflorescence are manifestly pubescent, distinguishing it from Panamanian species of *Witheringia*.

c. Plants glabrous to the naked eye; flowers solitary or paired ..... 8. *W. riparia*
cc. Plants manifestly pubescent to the naked eye; inflorescences many-flowered.
d. Flowers borne in stem fascicles on short, obscure peduncles; leaves toothed ..... 10. *W. stramoniifolia*
dd. Flowers borne on an elongate, more than 10 mm long peduncle; leaves entire ..... 4. *W. correana*
bb. Pubescence mostly of dendritic hairs.
e. Pedicels glabrate; flower buds elongate or ovoid ..... 6. *W. hunzikeri*
ee. Pedicels conspicuously shaggy pubescent; flower buds rotund .. 2. *W. bristaniana*
aa. Calyx truncate, teeth or lobes if present either formed as lateral or basal enations below the truncate apex or formed by splitting of the calyx wall in fruit.
f. Flowers mostly fascicled or solitary, the peduncles obscure and less than 8 mm long.
g. Calyx manifestly pubescent with dendritic hairs, other parts mostly tomentose or pilose.
h. Flowering calyx 4–5 mm long; corolla tube almost included in the calyx; Darién species ..... 2. *W. bristaniana*
hh. Flowering calyx less than 3 mm long; corolla tube well exserted from the calyx; upland species ..... 1. *W. asterotricha*
gg. Calyx glabrate or glabrous, hairs mostly simple; vegetative parts sparingly pubescent.
i. Flowers solitary or in pairs, calyx accrescent and enveloping the fruit until near maturity; anthers not apiculate ..... 8. *W. riparia*
ii. Flowers in fascicles of many blossoms, calyx not accrescent; anthers apiculate.
j. Calyx less than 2.5 mm long, without enations; lowland species ..... 9. *W. solanacea*
jj. Calyx more than 2.5 mm long; cloud forest species ..... 3. *W. coccoloboides*
ff. Flowers mostly on a distinct and elongate, more than 10 mm long peduncle.
k. Plants mostly glabrate; corolla glabrous within; anthers not apiculate; fruiting calyx not accrescent ..... 5. *W. cuneata*
kk. Plants mostly conspicuously pubescent; corolla with a ring of pubescence near the point of anther insertion, anthers apiculate.
l. Flowering calyx tubular, longer than broad, less than 2.5 mm long, becoming long pilose after fertilization; vegetative parts glabrous; anthers narrowly ovoid ..... 4. *W. correana*
ll. Flowering calyx broader than long, more than 2.5 mm long, not becoming more pubescent after anthesis; vegetative parts mostly pubescent; anthers often as broad as long ..... 7. *W. maculata*

1. **Witheringia asterotricha** (Standl.) Hunz., Kurtziana 5: 151–153. 1969.

Capsicum asterotrichum Standl. Publ. Field Columbian Mus., Bot. Ser. 4: 259. 1929. TYPE: *Cooper 576* (F, MO, NY).
C. multiflorum Standl. & Mort., Publ. Field Columbian Mus., Bot. Ser. 18: 1043–4. 1938. TYPE: Costa Rica, *Standley & Torres 51170* (F, US).

Large *herb* or *shrub* to 5 m tall, twigs shaggy pubescent with long, erect, dendritic, somewhat viscid hairs. *Leaves* elliptic or ovate, apically acute or acuminate, basally obtuse or rounded, to 25 cm long; above with scattered erect dendritic hairs, beneath softly tomentose especially along the veins, lateral veins 3–5 on each side of the midvein, the lamina reticulate veined; petioles 2–4 cm long, shaggy pubescent; minor leaves ¼ as large as the major leaves. *Inflorescences* mostly fascicled on short, less than 4 mm long obscure peduncles, rarely on elongate, slender peduncles 30 cm long; the pedicels 8–18 mm long, elongating slightly in fruit, mostly pubescent. *Flowers* with the calyces tomentose to glabrous, entire, to 2.0 mm long, in fruit becoming as long as 3 mm long and some-

times splitting; corolla mostly 5-merous, 5–9 mm long, the tube much shorter than the lobes, outside puberulent with short simple hairs or pilose with elongate, sometimes dendritic hairs, the lobes lanceolate, to 6 mm long, pubescent basally inside; filaments flattened, tomentose inside, almost as long as the anthers, the anthers elongoid, ca. 2 mm long, apiculate; the style slender, gently broadening upwards, glabrous, the stigma capitate. *Fruit* a red, mostly pubescent berry; seeds 1.4–1.6 mm long.

This is a species of moist upland forests. Collectors frequently refer to the purplish appearance of the stems and leaves which arises from a bluish cast to the leaf epidermis and from purplish hairs which cover the surface. It is recognizable by the hairy, purplish leaves and often pubescent fruits. Where it comes in contact with *W. solanacea*, chiefly in places where man has recently cut the forest, putative hybrids are found. In Colón on the Santa Rita Ridge, *W. asterotricha* is replaced by *W. hunzikeri*, which differs in its larger, toothed calyx. *Witheringia asterotricha* is confined to Panama and Costa Rica.

BOCAS DEL TORO: Farm 8 pasture, region of Almirante, *Cooper 576* (F). Between Quebrada and Gutierrez and E slope of La Zorra, headwaters of Río Mali, *Kirkbride & Duke 719* (MO). CHIRIQUÍ: Above Boquete, 4,800 ft, *D'Arcy 5440* (MO). Boquete, 5,500 ft, *Dwyer 6960* (MO). Premontane rain forest (oak) between Pinola and Quebrada Hondo toward summit on Chiriquí trail, *Kirkbride & Duke 888* (MO). COCLÉ: N (wet) rim of El Valle, *Allen 1822* (MO). Hills N of El Valle de Antón, 1,000 m, *Allen 2304* (MO). Cloud forest near La Mesa, *Croat 13360* (MO). Near La Mesa above El Valle, *Croat 14305* (MO). Cerro Pilón above El Valle, *Croat 14355* (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, cloud forest, *Duke & Dwyer 13932* (F, MO). El Valle, *Dwyer 1940* (MO). El Valle, near potato farm, *Dwyer 1984* (MO). Cerro Pilón, hill below summit, above El Valle de Antón, 2,000–2,700 ft, rain forest, *Dwyer et al. 4541* (MO). La Mesa to El Valle 2,000–2,500 ft, *Dwyer & Duke 8273* (MO.) Cerro Pilón, 2,700 ft, *Dwyer 8317* (MO). Cerro Pilón, La Mesa, *Dwyer 8332* (MO). El Valle, Cerro Pilón, *Kirkbride 1079* (MO). Cerro Pilón, 2,700 ft, *Lallathin 5056* (BIRM, G, MO). Mountains N of El Valle de Antón, 2,500–3,000 ft, cloud forest, *Lewis et al. 1715* (MO). Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte, very advanced secondary rain forest, *Lewis et al. 5481* (DUKE, MO), *5530* (MO). Foot of Cerro Pilón, rain forest, 2,000 ft, *Porter et al. 4354, 4466* (both MO). PANAMÁ: Cerro Campana, 2,300 ft, *Blum & Miller 2292* (MO, PMA). Cloud forest above Su Lin Motel, Cerro Campana, *Croat 14743* (MO). Cerro Jefe E slope, 2,700 ft. *Tyson 3580* (FSU, MO, MPU, WIS).

2. **Witheringia bristaniana** D'Arcy.[45] TYPE: Panama, *Duke & Elias E13689* (MO-2002010, holotype; BM, CORD, isotypes).—FIG. 31.

Shrub, twigs loosely tomentose with large, dendritic, stramineous hairs, glabrescent. *Leaves* broadly elliptic or ovate to 20 cm long, apically acuminate, basally rounded or obtuse and slightly oblique or dimidiate, above velutinous with erect, dendritic, ?viscid hairs, more densely so beneath; the petioles to 3 cm long, shaggy tomentose at least when young; minor leaves ca. ¼ as large as the

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[45] *Witheringia bristaniana* D'Arcy, sp. nov. Frutex ramunculis pilis dendriticis stramineis, laxe tomentosis, glabrescentibus, foliis late elliptica vel ovata usque ad 20 cm longa, supra velutina pilis dendriticis, dense infra, petiolis hirtis; inflorescentibus fasciculatis, floribus calyce cyathiformi 4–5 mm diametro longoque, breviter dentato, tomento de pilis dendriticis obruti; corollis campanulatis, extus pubescentibus pilis simplicibus previssimis, lobis 3–4 mm longis, staminibus aequalibus, antheris apiculatis. Nomen Narcisi Bristani, leguli plantarum Darinensium designatur ad hanc *Witheringiam*.

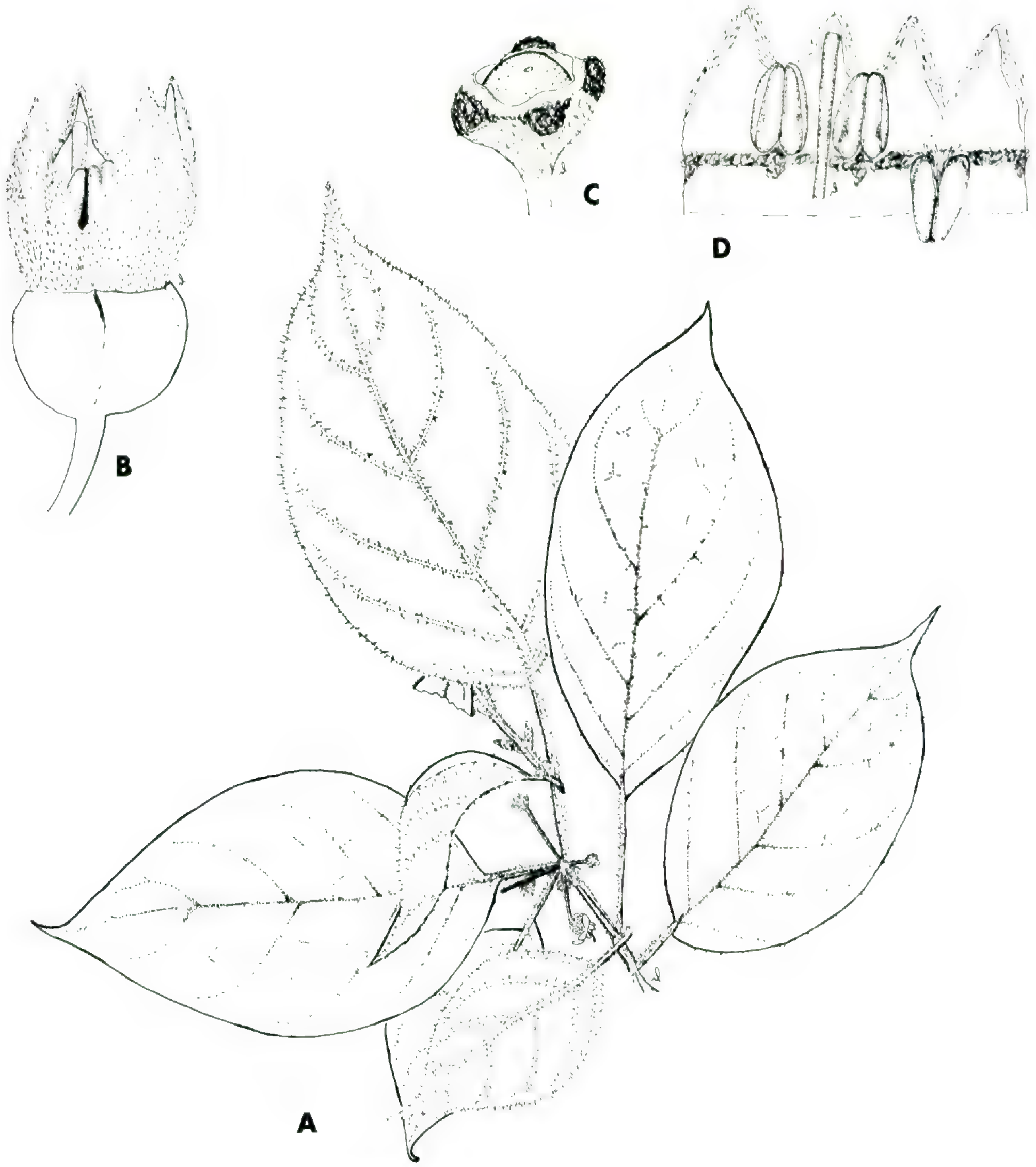

Figure 31. *Witheringia bristaniana* D'Arcy.—A. Habit with inflorescence (× ½).—B. Flower (× 5).—C. Immature fruit (× 5).—D. Opened corolla with 3 stamens and style (× 5). [After *Duke & Elias E13689* (MO).]

major leaves but otherwise similar. *Inflorescences* fascicled on short, 1–4 mm long, obscure peduncles; the pedicels filiform, shaggy pubescent, 15–20 mm long, perhaps glabrescent in fruit. *Flowers* with the calyx cyathiform, as broad as deep, 4–5 mm across, short-toothed, its detail obscured by the dense tomentum of erect, dendritic hairs; corolla companulate, pubescent outside with short simple hairs, inside perhaps pubescent at the point of anther insertion, lobed halfway down, the lobes 3–4 mm long, obtuse, reflexed, glabrous within; stamens equal, the filaments inserted near the mouth of the corolla tube, the anthers exserted, apiculate, the thecae opening wide and their walls folding back to back, the

anthers thus becoming elliptic, bright yellow with white margins; the style straight or curved, exserted ca. 2 mm, the stigma capitate, basally 2-lobed. *Fruit* not seen.

DARIÉN: Cloud and/or mossy forest, Cerro Pierre, 2,500–4,500 ft, shrub, fruits greenish, *Duke & Elias E13689* (BM, CORD, MO).

3. **Witheringia coccoloboides** (Dammer) Hunz., Kurtziana 5: 132–135. 1969.

Acnistus coccoloboides Dammer, Fedde Repert. 15: 389. 1917. TYPE: Colombia, *Triana* 2282 (?B, NY [fide Hunziker], not seen).
Brachistus fuscoviolaceus Cufod., Archiv. Bot. 10: 20. 1937. LECTOTYPE: Costa Rica, *Cufodontis* 397 (F).
Witheringia fuscoviolacea (Cufod.) Hunz., Kurtziana 5: 125–127. 1969.

Herb or *shrub* to 3 m tall, glabrate. *Leaves* elliptical, to 25 cm long, apically acute or acuminate, basally acute or obtuse; glabrate on both sides, beneath scurfy pubescent with degenerate dendritic hairs mostly on the veins; petioles to 2 cm long; minor leaves various. *Inflorescences* fascicled on obscure peduncles less than 4 mm long; the pedicels slender, glabrous or puberulent, ca. 1.5 cm long, becoming 3.5 cm long and erect in fruit. *Flowers* with the calyx cyathiform, narrowly campanulate or tubular, 3–6 mm long, the margin entire in flower and splitting in fruit, the calyx wall sometimes with 1–5 umbos or small teeth produced toward the base; corolla purple, white or pale yellow, 13–15 mm long, lobed ⅓–⅔ the way down, the lobes deltoid, 3 mm long, puberulent or glabrous outside, drying dark within, the tube puberulent near the apex within; filaments less than 1 mm long, tomentose, inserted at the top of the corolla tube, the anthers 2.0–3.5 mm long, broad at the base, apiculate, the broad connective dark and conspicuous when dry, partly exserted from the corolla tube; the style slender, gently enlarging upwards, stigma punctiform, sometimes oblique, exserted ca. 3 mm from the anthers. *Fruit* scarlet, obovoid or subglobose, ca. 8 mm long; seeds 2–3 mm long.

This species is distinguished by its puberulent to glabrous, not conspicuously pubescent vegetative parts, the succulent-appearing truncate calyx, the apiculate anthers and the sessile fascicles of flowers. It is similar to *W. solanacea*, but the calyx and corolla are larger and the anthers stouter. Sometimes there is an annulus or several umbos near the base of the calyx. Specimens with unusually longer calyces and shorter corolla tubes were recognized by Hunziker as *W. fuscoviolacea*. Plants from the Cerro Azul-Cerro Jefe area of Panamá Province frequently have coriaceous leaves and dry dark brown. In this area there is suggestion of hybridization with *W. solanacea*.

Witheringia coccoloboides occurs in Panama as a species of cloud forests from 300 to 2,500 m elevation. It is also reported from Colombia and from Costa Rica.

CHIRIQUÍ: Robalo Trail, N slopes of Cerro Horqueta, 6,000–7,000 ft, *Allen 4957* (MO). Rich cloud forests and adjacent clearing, Las Nubes W of Cerro Punta, *Busey 677* (ADW, BIRM, C, MO, MPU, PMA, UCWI). Along trail N of Cerro Punta, *Croat 10511* (MO). Above Cerro Punta, 7,600 ft, *D'Arcy 5358* (ADW, BIRM, C, F, MO, MPU, P, PMA, RSA, UCWI, W, WIS), *5376* (MO). Bajo Chorro, Boquete District, 6,000 ft, *Davidson 95, 290* (both MO, US). Premontane rain forest (oak between Pinola and Quebrada Hondo toward summit on Chiriqui Trail, *Kirkbride & Duke 916* (MO). Between Quebrada Hondo and

divide on Calderas-Chiriquicito Trail, cloud forest, *Kirkbride & Duke 953* (MO). Slopes of Volcán Horqueta near Boquete, Finca Collina, *Sullivan 415* (FSU). Cloud forest, Cerro Horqueta, 6,500 ft, *von Hagen & von Hagen 2050* (MO). Cerro Horqueta cloud forest, 6,500 ft, *von Hagen & von Hagen 2082* (MO). PANAMÁ: Cerro Jefe, E slope, 2,700 ft, *Blum & Duke 2182* (MO). Cerro Jefe, *Duke 9390, 9395* (both MO). Cerro Jefe, 2,900 ft, *Dwyer & Gauger 7336* (MO). Cerro Jefe, *Dwyer 8507* (MO). Forest in narrow valley between Cerro Azul and Cerro Jefe, *Foster 1146* (DUKE). In forest ca. 1 mi. upstream from Finca Indio, slopes of Cerro Jefe, *Foster & Kennedy 1854* (DUKE). Thick forest near top of Cerro Jefe, 900 m, *Foster & Kennedy 1879* (DUKE). Cerro Jefe, 800–1,000 m, *Gentry 6779* (ADW, BIRM, C, MO, UCWI). Cerro Jefe E slope in "*Clusia*" cloud forest, *Tyson 3403* (SCZ). Top of Cerro Jefe, 2,700–3,000 ft, *Tyson et al. 4403* (MO), *4413* (FSU, MO). Slopes of Cerro Jefe beyond Cerro Azul ca. 5.5 mi. towards La Eneida, 2,700–3,000 ft, *Wilbur & Teeri 13640* (DUKE).

4. **Witheringia correana** D'Arcy.[46] TYPE: Panama, *Dressler 4053* (MO).

Herb to 1 m, stems stout, glabrous, soft, drying green with conspicuous furrows. *Leaves* to 30 cm long and 15 cm broad, obovate, apically acuminate, basally obtuse or acute, membranaceous, glabrous when expanded but with minute, stout, simple hairs when emerging, principal veins 5–9 on each side of the midvein, slender, stramineous and elevated beneath; the petioles 3–5 cm long, glabrous, slightly clasping at the base. *Inflorescences* corymbose or subumbellate on a nearly straight, erect, 3–5 cm long peduncle, flushed with purple and bearing a regularly spaced, open cicatrix along one side from apex to base; pedicels slender, glabrous, purple and ca. 10 mm long but becoming yellowish or green, 20 cm long and thickening upwards in fruit. *Flowers* tetramerous, the calyx purple, cyathiform, truncate, 2 mm long, with scattered white, crumpled simple hairs, after anthesis becoming conspicuously long pilose with eglandular but perhaps viscid hairs, attaining 7–10 mm and loosely enveloping the fruit, tardily splitting in about 3 sutures to expose the fruit; the corolla yellowish, 5–7 mm long, outside with minute simple hairs, glabrous within, the united portion tubular, exceeding the calyx, lobed about halfway down, the lobes obtuse, the stamens inserted near the top of the corolla tube, the filaments ca. 0.8 mm free, tomentose above the point of insertion, becoming broad, flattened, and erose margined in the lower portion of the corolla tube, the anthers 3.5 mm long, light yellow with a prominent, light colored apicule, slightly exserted; the stigma small, exserted ca. 2 mm beyond the anthers. *Fruit* a glabrous orange berry 10 mm across, ultimately filling and rupturing the enveloping calyx; the seeds fabiform, 2.5 mm across, the surface a reticulum of polygonal cells, yellow, green or stramineous.

This species is distinct in its accrescent, pilose calyx, in its large leaves, and in the structure of the inflorescence. The pubescence resembles that of *W.*

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[46] *Witheringia correana* D'Arcy, sp. nov. Herba 1 m alta, caule crasso, glabro, in sicco viride, foliis amplis usque ad 30 cm longis, 15 cm latisque, obovata, tenuia, glabra; inflorescentibus corymbosis vel umbellatis; pedunculo recto 3–5 cm longo, facie unica cicatricosa; pedicellis glabros, purpureis, 10 mm longis, accrecentibus usque ad 20 mm longis; floribus tetrameris, calyce purpureo, 2 mm longo, pilos albos dispersos gerenti, post anthesin accrescenti usque ad 7–10 mm, dense longipiloso, acinum laxe involventi; corollis 5–7 mm longis extus minute pubescentibus, intus glabris; antheris 3.5 mm longis, apiculatis; acinis coccineis; seminibus reticulatis, 2.5 mm diametro. Nomen Mireyae D. Correae A. legulae plantarum Panamensium designatur ad hanc *Witheriangiam*.

maculata, but the flowers are much smaller. The seeds are those of sect. *Witheringia* (see Hunziker, 1969: 106).

Witheringia correana is known only from the type collection, taken in a high rainfall (6,000+ mm) area near the Caribbean coast and just east of the Canal Zone.

COLÓN: Wet forest near Río Gauche, plant ca. 1 m tall, flowers yellow, fruit red, *Dressler 4053* (MO).

5. **Witheringia cuneata** (Standl.) Hunz., Kurtziana 5: 118–122. 1969.

Lycianthes cuneata Standl., Publ. Field Columbian Mus., Bot. ser. 4: 260. 1929. TYPE: Panama, *Cooper 405* (F, NY, US).
L. austin-smithii Mort. & Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1057. 1938. TYPE: Costa Rica, *Austin-Smith* 4117 (F).
L. inaequalis Mort. & Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1059–60. 1938. TYPE: Panama, *Dunlap 396* (F, US).
L. chiriquensis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 100–101. 1940. TYPE: Panama, *Davidson 623* (A, F).
L. laxissima Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 169–70. 1940. TYPE: Panama, *Davidson 67* (F, holotype; MO, isotype).

Herb or *shrub* to 3 m tall, glabrate; twigs slender, some with minute, ascending hairs (visible with a lens). *Leaves* irregular in shape, mostly strongly oblique, oblong, elliptical, ovoid or obovoid, to 25 cm long, membranaceous, glabrous; the petioles slender, short, to 1.5 cm long; minor leaves rotund. *Inflorescences* fascicles or subumbellate on branched peduncles to 3 cm long, the ultimate branches of the peduncle slender; the pedicels slender, 1–1.5 mm long. *Flowers* with the calyx small, campanulate, glabrous, the apex truncate, sometimes with 4–5 angles at the apex; the corolla obconical, the tube 2–3 mm long, glabrous outside, pubescent at the top within, lobed a little more than halfway down, the lobes lanceolate, 3–4 mm long, glabrous; filaments fine puberulent, inserted at the top of the corolla tube, the anthers 2.2–3.6 mm long, not apiculate; the style slender, broadening slightly upwards, ultimately 8 mm long. *Fruit* large, globose, ca. 10–12 mm across.

Witheringia cuneata is almost glabrous, but with the aid of a good lens minute ascending hairs may be seen on the twigs. The slender peduncles and small flowers are also distinctive. Most collections seen have very strongly oblique leaves, but the overall shape is very variable.

Known in Panama only from the Chiriquí Mountains and their Caribbean drainage, the species is reported from Nicaragua to Venezuela. It is apparently a plant of middle and upper elevations.

BOCAS DEL TORO: Lincoln Creek, *Carleton 85* (US). Research Lagoon, Region of Almirante, *Cooper 405* (F). Changuinola Valley, *Dunlap 85A* (F). Changuinola Valley, *Dunlap 396* (F, US). Changuinola River, near Chiriqui Lagoon, *von Wedel 2601* (MO). CHIRIQUÍ: Bajo Chorro, Boquete District, 6,000 ft, *Davidson 66* (A). Rain forest, Bajo Chorro, Boquete District, 6,000 ft, *Davidson 67* (F, MO). Rain forest, Bajo Chorro, 6,000 ft, *Davidson 414* (A, MO). Forest, Boquete, 3,800 ft, *Davidson 623* (F). Cerro Horqueta rain forest, 6,500 ft, *von Hagen & von Hagen 2081, 2082* (both MO). Near Bajo Chorro, 1,900 m, *Woodson & Schery 671* (MO).

6. **Witheringia hunzikeri** D'Arcy.[47] TYPE: Panama, *Lewis et al.* 5258 (MO-1984206, holotype).

Herb or *subshrub* to 3 m tall, stems and twigs fistulose, pubescent with ?viscid, dendritic, more or less persistent hairs. Leaves broadly ovate or elliptic, to 20 cm long, apically acute or acuminate, basally obtuse, sometimes somewhat oblique, above with scattered simple and dendritic hairs, beneath softly tomentose with dendritic hairs, lateral veins strongly ascending and almost straight, ca. 5 on each side of the midvein; the petioles 3–6 cm long, shaggy pubescent with dendritic hairs; minor leaves rotund, ca. ⅓ as large as the major leaves. *Inflorescence* a dense many-flowered fascicle, the peduncle obscure, 1-to several-branched, the branches less than 4 mm long with a cicatrix of large pedicel scars; the pedicels filiform, 10–15 mm long, glabrate. *Flowers* 4-merous; the calyx 3–4 mm long, slightly longer in fruit, densely tomentose outside, glabrous within, the lobes unequal, 0.8–1.6 mm long, deltoid; the corolla yellowish, densely fine puberulent outside with minute, simple hairs, urceolate, the tube and limb short, not exceeding the calyx, the lobes obtuse, spreading or reflexed, ca. 4 mm long, glabrous within; stamens sometimes somewhat unequal, the filaments relatively stout, glabrous, the anthers ovoid, yellow, apiculate or not; ovary and style sometimes glabrous, the style exserted ca. 2 mm, the stigma of two appressed, ovate lobes, smooth. *Fruit* globose, pubescent, red, ca. 6 mm across.

The lobed calyx places this species in sect. *Brachistus*, but the calyx is accrescent to a much lesser degree than other members of this section. At first glance, *W. hunzikeri* resembles *W. asterotricha*, but the flowers are smaller and the calyx is distinctly lobed.

All collections seen are from the same locality, Santa Rita Ridge, a region within 20 km of the Caribbean and about the same distance east of the Canal Zone. Rainfall is high (5,000+ mm) with little seasonal variation; the elevation is less than 900 m.

COLÓN: Santa Rita Ridge, 5 mi. from highway, *Croat 13182* (MO). Santa Rita lumber road ca. 15 mi. E of Colón, *Dressler & Lewis 3719* (MO, SCZ, UCWI). 8 mi. E of Santa Rita Ridge, 800 ft, *Dwyer et al. 9022* (MO). Santa Rita, cuadro de muestreo no. 1, en zona de selvas altas perennifolias sobre suelos rojos lateriticos, arcillosos, 200–300 m, *Gomez-Pompa et al. 3160* (MO). Santa Rita Ridge, 4–5.5 mi. E of Transisthmian Highway, advanced secondary forest, *Lewis et al. 5258* (MO). Santa Rita Ridge, end of road from Transisthmian Highway ca. 10 mi. from highway, advanced secondary forest, *Porter et al. 4782* (MO, NY).

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[47] *Witheringia hunzikeri* D'Arcy, sp. nov. Herba frutexve usque ad 3 m altus pilis dendriticis persistentibus pubescens. Foliis ovatis vel ellipticis usque ad 20 cm longis, subter molliter tomentosis; inflorescentia fasciculata, multiflorida, pedunculo obscuro, brevissimo, furcata, cicatricoso, pedicellis gracillimis, glabratis 10–15 mm longis; floribus 4-meri; calyce 3–4 mm longo parum accrescenti extus dense tomentoso lobis deltoideis parum inaequalibus 0.8–1.6 mm longis; corolla flavida, urceolata, extus puberulenta pilis minutis simplicibus, tubo brevi calycem non exceedenti, lobis 4 mm longis, intus glabris; staminibus vix aequalibus, filamenta crassis, glabris, antheris ovoideis, interdum apiculatis; pistillo interdum glabro; acinis rubris, diametro 6 mm. Nomen Armando T. Hunzikeri, Cordovensis, scrutioris generis *Witheringiae* designatur hanc *Witheringiam*.

7. **Witheringia maculata** (Mort. & Standl.) Hunz., Kurtziana 5: 117–118. 1969.

Capsicum maculatum Mort. & Standl., Field Mus. Nat. Hist., Bot. Ser. 18: 1043. 1938. TYPE: Costa Rica, *Skutch 3335* (F, MO, NY).
C. macranthum Standl. & Mort., Field Mus. Nat. Hist., Bot. Ser. 18: 1042. 1938. TYPE: Costa Rica, *Standley & Valerio 51906* (F, US).
Witheringia macrantha (Standl. & Mort.) Hunz., Kurtziana 5: 114–117. 1969.

Erect *herb* to 2 m tall, stems succulent, pilose with simple hairs. *Leaves* broadly ovate or elliptical to 20 cm long, pilose to glabrate, above with scattered erect hairs on the lamina, beneath mostly pilose along the veins, apically short acuminate, basally obtuse to rounded or subcordate; petioles short, to 2 cm long, minor leaves rotund ca. ¼ as long as the major leaves but occasionally much reduced or tardily emergent. *Inflorescences* few- to many-flowered fascicles or subumbellate on short or elongate, stout or slender, simple or branched, sometimes bracteate peduncles, these manifestations sometimes all on the same plant; pedicels 1–3 cm long, pubescent, elongating slightly in fruit. *Flowers* with the calyx 3–6 mm long, broader than long, urceolate, pilose to glabrate, the apex entire and manifestly contracted, especially in fruit, subtended by a conspicuous continuous or interrupted evagination of the calyx wall which on the herbarium sheet may appear as a large backward directed collar or teeth and cause the calyx margin to appear undulate or lobed; corolla large and showy, cream colored, often with broad ribs of purple or green on the outside, pilose to glabrate, the hairs white, the united portion short-campanulate and angled, the lobes 10–15 mm long, slightly concave dorsally, narrowly deltoid, approximate and forming a cup, glabrous within except for a ring of pubescence at the point of filament insertion; the filaments short, pilose, inserted at the top of the corolla tube (limb), the anthers yellow with conspicuous dark connectives on the dorsal (abaxial) surface, broadly ovate or pyriform, apiculate, 3–6 mm long, partly exserted, the stigma included. *Fruit* (immature) depressed globose (oblate), glabrous with a conspicuous terminal stylar scar, the basal half loosely enclosed by the calyx.

This species is strikingly different from all other Panamanian species of *Witheringia* in its large, attractive corolla, succulent-appearing calyx and broad anthers. It is closely related to *W. dichotoma* (Rusby) D'Arcy of Colombia, which has different leaf venation and narrowly ellipsoid anthers.

In spite of its striking overall appearance, *W. maculata* merely represents extremes of several morphological trends in the genus and no important departure. Its variability is also unusual. The great range of corolla and anther size and shape, and the uncorrelated variability of pubescence on calyx and corolla in the same population or sometimes the same plant argue very strongly for caution in recognizing more than one taxon under this species.

Witheringia maculata has been found only in the mountains of Costa Rica and Chiriquí. It is a plant of mature forests of upper elevations.

BOCAS DEL TORO: Between Quebrada Gutierrez and E slope of La Zorra, headwaters of Río Mali, Chiriquí Trail, *Kirkbride & Duke 724* (MO). Chiriquicito-Caldera Trail between Quebrada Higueron and Gutierrez, *Kirkbride & Duke 764A* (MO). CHIRIQUÍ: In forest above Boquete, 5,200 ft, *D'Arcy 5472* (MO, MPU). Rain forest, Bajo Chorro, Boquete District, 6,000 ft, *Davidson 289* (MO, US). Cerro Horqueta cloud forest, 6,500 ft, *von Hagen & von Hagen 2103* (MO). Near Bajo Chorro, 1,900 m, *Woodson & Schery 673* (MO).

8. **Witheringia riparia** Kunth *in* H. & B., Nov. Gen. Sp. 3: 16. 1818. TYPE: Colombia, *Bonpland s.n.* (P).—FIG. 32.

Solanum davidsoniae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 103–4. 1940. TYPE: Panama, *Davidson 362* (A, MO, US).

Shrub or *tree* to 4.5 m tall, glabrate; twigs glabrous, much branched, soon somewhat corky, the nodes enlarged. *Leaves* lanceolate or elliptic, mostly oblique, apically acuminate, basally acute or acuminate, to 13 cm long, membranaceous, mostly drying with a crinkled, mottled appearance above, glabrous or with scattered short simple hairs on the lamina above, somewhat upfolded from the midrib, veins 3–5 on each side of the midrib; the petiole short, to 10 mm long; minor leaves apically obtuse, ca. ¼ as large as the major leaves. *Inflorescence* a 1- to few-flowered fascicle arising without evident peduncle; the pedicel slender, enlarging slightly upwards, to 2 cm long, glabrous, becoming somewhat stouter and longer in fruit. *Flowers* with the calyx 4–5 mm long, obconical, angled, with 5 short umbos or teeth emerging from the angles, basally slightly oblique, glabrous, accrescent and investing the entire fruit except at the open but somewhat contracted apex, the teeth not enlarging; corolla greenish yellow, 10–13 mm long, campanulate, the tube or limb short, 4–5 mm long, lobed ⅔ the way down, the lobes obtuse, 6–9 mm long, puberulent inside and out in the apical portion; filaments inserted at the bottom of the limb, pubescent inside, free ca. 1 mm, laterally with ascending tufts of hairs at the point of insertion, anthers somewhat unequal, oblongoid, basally hastate, not apiculate, ca. 3.5 mm long; the style slender, cylindrical, green. *Fruit* ovoid, 10–12 mm long, enclosed except at the apex by the accrescent calyx.

This is an uncommon species of upland Central America and north South America. The flowers are greenish yellow to white, and in fruit the 5-ribbed calyx tightly invests the lower portion of the berry, perhaps ultimately splitting.

CHIRIQUÍ: Finca Collins near Boquete, *Blum & Dwyer 2535A* (MO, SCZ). Edge of pasture above Boquete, 5,200 ft, *D'Arcy 5460* (MO). Above Boquete, 5,200 ft, *D'Arcy 5473* (MO). Rain forest, Bajo Chorro, Boquete District, 7,000 ft, *Davidson 362* (F, MO, US). Premontane rain forest (oak) between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke 913* (MO). In damp places, forests along the Río Ladrillo above El Boquete, 1,200–1,300 m, *Pittier 3170* (US). Quebrada Velo 1,800 m, *Woodson & Schery 259* (MO). Cerro Horqueta cloud forest 6,500 ft, *von Hagen & von Hagen 2065* (MO).

9. **Witheringia solanacea** L'Her., Sert. Angl. 33, *tab. 1.* 1788. TYPE: (not seen).[48]

Witheringia macrophylla H. & B. *ex* Dun., Sol. Syn. 1. 1816. TYPE: Colombia, *Bonpland s.n.* (P).
Solanum panamense van Heurck & Müll.-Arg., Obs. Bot. 128. 1871. TYPE: Panama, *Fendler 251* (G, GH, K, MO, US).
Brachistus meianthus Donn. Sm., Bot. Gaz. (Crawfordsville) 57: 424. 1914. TYPE: Guatemala, *von Tuerckheim 1134* (GH, US).
Capsicum macrophyllum (Dun.) Standl., Jour. Washington Acad. Sci. 17: 16. 1927.
C. stenophyllum Mort. & Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1044. 1938. TYPE: Costa Rica, *Stork 2663* (F).

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[48] For a full list of synonyms see Hunziker (1969: 137–8). Only the above names have been used for Panamanian material.

FIGURE 32. *Witheringia riparia* Kunth.—Right. Habit with flower and buds (× ⅗). [After *Blum & Dwyer 2535A* (MO).]—Left. Fruit; the calyx is appressed tightly to the berry and its height is variable (× ⅗). [After *D'Arcy 5457*, pickled material (MO).]

C. tetramerum Standl. & Mort., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1045. 1938. TYPE: Costa Rica, *Skutch 2862* (MO, NY; holotype US, not seen).

Herbs, shrubs or *trees* to 4 m tall, erect or sprawling, sometimes blooming and fruiting on turoins only 20 cm tall; twigs puberulent with mostly simple or glandular and occasionally dendritic hairs. *Leaves* ovate or elliptic, to 20 cm long, apically acute or acuminate, basally obtuse or rounded, sometimes dimidiate, above glabrate with scattered simple hairs, beneath glabrate to tomentose with erect hairs mostly on the veins, membranaceous, seldom drying dark; the petiole to ⅓ as long as the leaf, puberulent; minor leaves present or wanting, often equalling the major leaves. *Inflorescence* a many-flowered fascicle on short, obscure peduncles; the pedicels mostly puberulent, slender, ca. 10 mm long. *Flowers* with the calyx very small, to 2 mm long but mostly much shorter, not enlarging in fruit, but sometimes splitting, pubescent or not, the apex truncate; the corolla 4–5-merous, rotate, the tube 1–3 mm long, always much shorter than the lobes, puberulent outside and with a ring of hairs at the apex within, the lobes obtuse to lanceolate, 3–6 mm long, puberulent outside, glabrous within, yellow, brown or green, often spotted; filaments short, flattened, tomentose on the ventral surface, the anthers ovate to oblongoid, mostly 2–3 mm long, longer than the filaments, apiculate, the connective conspicuous on the dorsal surface or not. *Fruit* orange to scarlet, glabrous or pubescent, globose or obovoid, juicy, ca. 8 mm long but very variable in size within a single fascicle, elevated above the leaves, stone cells sometimes present; seeds 1–1.5 mm long, yellow.

This species may be recognized by the fascicled flowers and minute calyces. *Witheringia cuneata* is the only other Panamanian species of *Witheringia* with such small calyces, and the inflorescences of that species are mostly pedunculate and fewer-flowered. The pedicels of *W. cuneata* are thinner as well. *Witheringia solanacea* is the most widespread species of the genus, occurring from Mexico to Brazil and in the Antilles. It is the only widespread and common species of *Witheringia* in lowland Panama, and although it ascends to upper elevations, upland plants are often suggestive of introgression from other species.

Witheringia solanacea displays great variability of aspect, pubescence, and flower color. This variability together with probable hybridization with other taxa makes definition of useful segregates difficult. Hunziker (1969: 153) questioned whether *W. asterotricha* should be considered a variety of *W. solanacea* or a distinct species. Many plants from recently disturbed areas of former upland forest are intermediate between *W. solanacea* and *W. asterotricha* in coloration and pubescence, and the calyces are slightly larger than those of either presumptive parent. The series of D'Arcy collections from Chiriquí (cited below) are from populations of this sort, and the type collection of *Capsicum stenophyllum* is very similar. Plants of reduced pubescence and slightly larger calyces than usual were placed by Hunziker under *W. meiantha*. Such collections from scattered localities are not otherwise separable from typical *W. solanacea* and do not represent a distinct taxon. *Witheringia solanacea* seems to hybridize with *W. coccoloboides* in the Cerro Jefe area.

The name of this species is based on a description and plate which were

prepared from living cultivated material, and while no specimen has been found to serve as a lectotype, Hunziker was able to see representative specimens at Kew (K). L'Heritier's description differs in some details from plants now considered under this name, but his protologue appears to refer to the species treated here.

BOCAS DEL TORO: Daytonia, Region of Almirante, *Cooper 136* (US). Changuinola Valley, *Dunlap 409* (US). Río Teribe between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 480* (MO). Near Chiriquí Lagoon, *von Wedel 1264* (US). Old Bank Island, Chiriquí Lagoon, *von Wedel 2125* (MO, US). Near Nievecita, 0–50 m, *Woodson et al. 1852* (GH, MO). CANAL ZONE: Ca. 2 mi. S of Fort Sherman, *Blum & Tyson 2009* (FSU, MO, SCZ). 3 mi. SW from Gatún locks, along road S-9, *Correa 217* (MO, PMA). Road S-11 NW of Escobal, *Croat 12467* (MO). Under Río Coco Solo bridge, Transisthmian Highway near Colón, *D'Arcy 5173* (MO). Pipeline Road within 5 mi. of Gamboa Gate, *D'Arcy & D'Arcy 6209* (MO). Near Hill C-6, Fort Sherman, *Duke 4384* (MO). Fort San Lorenzo Navy Reservation, cutover second growth, *Ebinger 478* (MO, US). Chagres, *Fendler 251* (G, GH, K, MO, US). Gatún, *Ostenfeld 43* (C). Near Gatunsillo, *Piper 5600* (US). Frijoles, *Standley 27618* (US). Cascadas plantation near Summit, *Standley 29636* (US). Between France Field and Cativa1, *Standley 30215* (US). Wet field, Frijoles, *Standley 31478* (C, US). Old Fort San Lorenzo, *Tyson 2211* (FSU, MO). Fort San Lorenzo, *Tyson & Blum 3696* (SCZ). Boy Scout camp on Madden Lake, *Tyson 5448* (FSU, MO). Cocoli Island, Miraflores Lake, *White 295* (MO, US). Barro Colorado Island, *Aviles 119* (MO); *Croat 4073, 4080, 5964, 6391, 6721, 6785, 6906, 9032, 11835, 12180, 12199* (all MO); *Ebinger 558* (MO); *Shattuck 77* (F, MO), *160* (GH, MO), *800* (MO); *Standley 40856* (US). CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1,500–2,000 m, *Allen 1581* (MO, US). Nueva California, *D'Arcy 4253A* (MO). In abandoned, shrubby, fenced pasture between Concepción and El Hato de Volcán, *D'Arcy 4255* (MO). Between El Volcán and Concepción, *D'Arcy 4263* (MO). In cafetal, Los Naranjos, *D'Arcy 4268* (MO). Abandoned cultivation S side of Cerro Pando, 6,000 ft, *D'Arcy 5389* (MO). Low weedy area, N side of Cerro Pando, 6,000 ft, *D'Arcy 5408* (MO). Above Boquete, 5,000 ft, *D'Arcy 5458* (MO). Boquete, 3,800 ft, *Davidson 587* (A, F). Pastures around Boquete, 1,000–1,300 m, *Pittier 3044* (MO, US). Along Río Dupí near sea level, *Pittier 5436* (US). Río Chiriquí to Remedios, 15–50 m, *Woodson et al. 1181* (A, MO). COCLÉ: Near La Mesa above El Valle, *Croat 14380* (MO). El Valle, *Dwyer 1983* (MO). El Valle de Antón at foot of Cerro Pilón, 2,000 ft, cloud forest, *Dwyer & Correa 7934, 7968* (both MO). Hills NE of El Valle de Antón, 2,000 ft, disturbed forest edges, *Lewis et al. 1691, 1697* (both MO). El Valle de Antón, 1,000–2,000 ft, edge of cloud forest and roadside, *Lewis et al. 2615* (MO, UCWI). Foot of Cerro Pilón above El Valle de Antón, 2,000 ft, rain forest, *Porter et al. 4633, 4643* (both MO). Between Las Margaritas and El Valle, *Woodson et al. 1290* (GH, MO). COLÓN: South of Portobelo 2 mi. along river, *Croat 11417* (MO). Street weed, Portobelo, *D'Arcy 4056* (MO). Weed along overgrown fenceline, Portobelo, *D'Arcy 4060* (MO). DARIÉN: Near Boca de Cupe, 40 m, *Allen 872* (GH, MO, US). Río Tuqueza below Quebrada Venado, *Bristan 1072* (MO, WIS). Río Chico, Yaviza to ca. 1 hour upstream by outboard, secondary forest in swamps and hillsides, *Burch et al. 1081* (GH, MO). Canglón near the river, *Duke & Bristan 361* (MO). Hill near Río Chucunaque ca. 4 mi. below Yaviza, *Duke 4871* (MO). 10 mi. S of El Real on Río Pirre, *Duke 5455* (MO). Agua Fría ca. 8 mi. N of Santa Fé, 50 m, *Duke 10110* (MO, WIS). Near Refugio, 15–21 mi. N of Santa Fé, 30 m, *Duke 10308* (US, WIS). Cuipo forests near Santa Fé, *Duke 12283* (WIS). Río Mortí in premontane rain forest, 229 ft, *Duke 15420* (WIS). Premontane rain forest at Camp Summit, near San Blas border, *Duke 15483* (WIS). Camp Dubaganala in premontane rain forest, 1,371 ft, *Duke 15500* (WIS). Cocalito, beach area, *Dwyer s.n.*, 1963 (MO). Tres Bocas on Río Cuasi, *Kirkbride & Duke 1362* (MO). Camp Summit by Darién-San Blas border along Sea Level Canal Route 17, 100–1,200 ft, seasonal evergreen forest and weedy clearing, *Oliver et al. 3675* (MO). Near Paya, Río Paya, *Stern et al. 270* (MO, US). Near Campamento Buena Vista, Río Chucunaque above confluence with Río Tuqueza, *Stern et al. 850* (MO, US). Cana-Cuasi Trail, Chepijana District, 8,000 ft, *Terry & Terry 1622* (A, F). LOS SANTOS: Guayabo, a place several mi. W of Tonosí, vegetation second growth, riverine, *Stern et al. 1895* (MO). PANAMÁ: Cerro Azul 5 mi. N on road to Cerro Jefe, 2,400 ft, *Blum et al. 1743* (FSU). Road to Cerro Jefe ca. 7 mi. N of Cerro Azul, 2,600 ft, *Blum et al. 1765* (FSU, SCZ, US). Cerro Jefe, E slope, 2,700 ft, *Blum & Duke 2193* (FSU, MO). Along road to Cerro Jefe 10 mi. S from Goofy Lake, *Correa & Dressler 155* (MO). Region

of Cerro Jefe, 1,000 m, edge of forest, *Correa et al. 1606* (MO). Near Cerro Azul, 3 mi. above Goofy Lake, *Croat 11572* (MO). Road past Cerro Jefe toward La Eneida, *Croat 13099* (MO). Plentiful in cafetal, Finca del Indio, Cerro Jefe, *D'Arcy 5227* (L, MO, P, WIS). Cerro Campana, *D'Arcy & Dressler 5495* (MO, NY). Along Pan-Am Highway, open grazed area near Jenine, Río Cañita, *Duke 3850* (MO). Woods along Pan-Am Highway halfway between El Llano and Río Mamoní, *Duke 5638* (MO). Cerro Azul, *Duke 9343* (MO, OS), *9377* (MO). Forest along headwaters of Río Corso off Río Pacora, 500 m, *Duke 11911* (MO, WIS). Cerro Azul, 2,000 ft, *Dwyer 2064* (MO). Goofy Lake to 8 mi. S of Goofy Lake toward Cerro Azul, *Dwyer 7059* (GH, MO). Goofy Lake to 1.5 mi. S of Goofy Lake, 1,800 ft, roadside thicket, *Dwyer & Hayden 8024* (MO). Between Cerro Jefe and Eneida, 2,100–2,900 ft, *Dwyer et al. 8212* (MO). Cerro Jefe to 3,100 ft, *Dwyer & Gentry 9471* (MO). Cerro Jefe and forests along road beyond summit, *Hayden 1017* (MO). Road to Cerro Jefe, 2–3 mi. S of Goofy Lake, 2,000–2,200 ft, *Lewis et al. 224* (MO, US), *283* (G, H, K, MO, UC, US). SE slope of Cerro Campana, roadside and grassland, *Lewis et al. 3150* (MO). 1 mi. N of Goofy Lake, edge of cultivated field, *Oliver 2675* (MO). Along Charave River near Chepo, 50–200 m, *Pittier 4711* (F, MO, US). Cerro Azul, roadside woods and thickets, *Porter et al. 4121* (MO). Cerro Campana above Su Lin Motel, rain forest, *Porter et al. 4260* (MO). Summit of Cerro Campana, rain forest, *Porter et al. 4898*, (ADW, MO, MPU), *4949* (MO). Río Tapia, *Standley 26209* (US). Río Tocumen, *Standley 26727* (US). Río Tapia, *Standley 28158* (US). Río Tocumen, *Standley 29481* (US). Juan Díaz, wet thicket, *Standley 30538* (C, US). Cerro Jefe in "*Clusia*" forest, 2,700–3,000 ft, *Tyson et al. 3322* (MO). 1 mi. N of Cerro Azul, 2,300 ft, *Tyson & Blum 4076* (FSU, MO). Cerro Azul, *Wendehake 4* (MO, PMA). Cerro Campana near Su Lin Motor Lodge, 3,000 ft, *Woods & Woods*, 1967 (DUKE). SAN BLAS: Hills SW of Puerto Obaldía, edge of disturbed area, *Croat 16705* (MO). Near Puerto Obaldía, *Croat 16981* (MO). Headwaters of Río Cuadi, Camp Diablo, seasonal evergreen forest along river, 273.4 ft, *Duke et al. 3642* (MO).

10. **Witheringia stramoniifolia** Kunth *in* H. & B., Nov. Gen. 3: 1818. TYPE: *Herb. Bonpland s.n.* (P; MO, photo).[49]

Brachistus stramoniifolius (Kunth) Miers, Ann. Mag. Nat. Hist., Ser. 2. 3: 263. 1849. (Type species of *Brachistus* Miers; of *Witheringia* sect. *Brachistus* (Miers) Hunz.).
Capsicum stramoniifolium (Kunth) O. Kuntze, Rev. Gen. Pl. 2: 450. 1891.
C. malacophyllum Standl., Publ. Field Columbian Mus., Bot. Ser. 4: 260. 1929. TYPE: Mexico, *Mexia 1780* (MO).
Bassovia stramoniifolia (Kunth) Standl., Contr. U. S. Natl. Herb. 23: 1303. 1924.

Shrub or *tree* to 6 m tall; twigs puberulent with small, dense, mostly appressed, simple or glandular hairs. *Leaves* broadly ovate, to 25 cm long, sinuately 1–4-dentate on each side of the margin, occasionally entire, the apex and lobes acuminate, the base mostly truncate, slightly dimidiate, the veins and lamina softly pubescent with fine erect hairs, more conspicuous beneath; the petiole to ½ as long as the leaves, pubescent; minor leaves mostly present, less than ½ as large as the major leaves. *Inflorescences* several-flowered, fascicled in the leaf axils, peduncles not apparent, the pedicels ca. 10 mm long, pubescent and deflexed in flower, glabrescent, elongating and erect in fruit. *Flowers* with the calyx cyathiform, as broad as deep, ca. 4 mm long with five manifest acuminate lobes ca. 1 mm long, pubescent, drying with evident venation, accrescent and partly or entirely enclosing the fruit; corolla yellow, 7–9 mm long, the tube puberulent outside and in the upper portion, lobed ⅓ way down or further, the lobes puberulent outside, obtuse; filaments puberulent on the ventral surface, inserted in the middle of the corolla tube or above, somewhat shorter than the

[49] For a full list of synonyms see Hunziker (1969: 154–6). The above are the only names which have been used for Panamanian material.

anthers, the anthers oblongoid, mostly not apiculate, 2–3 mm long, exserted. *Fruit* compressed globose, loosely enveloped by the calyx, ca. 10 mm across.

This species is readily distinguished from other Panamanian species by its dentate leaves and the accrescent, toothed calyx. Apparently native to Mexico, there are outlying reports for this species from El Salvador, Costa Rica, and Panama. There is only one known collection from Panama. *Witheringia stramoniifolia* is apparently a species of middle elevations. Examination of material from a wide geographic range suggests that several taxa may be confused under this one name.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 600–7,000 ft, herb 8 ft, flowers greenish white, *Allen 4955* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 172. BIGNONIACEAE[2]

ALWYN H. GENTRY[3]

Woody *trees*, *shrubs*, or *vines*, rarely herbaceous; outer scales of axillary buds often pseudostipular and sometimes foliaceous; glandular fields often present between the petioles and rarely at the petiole apex. *Leaves* usually opposite, palmately or pinnately compound, sometimes simple, the terminal leaflet often replaced by a tendril. *Inflorescence* terminal or axillary, a panicle or raceme, sometimes reduced to a fascicle or a single flower. *Flowers* with the calyx synsepalous, usually more or less cupular, truncate to variously lobed or spathaceously split; corolla sympetalous with a conspicuous tube and 5 usually imbricate lobes; stamens inserted on corolla tube, didynamous, usually 4, rarely 2, a posterior staminode usually present, anthers with 1 or 2 thecae, these usually divergent or divaricate and held against the adaxial side of corolla tube, the filaments slender, ovary superior, 1 or 2 locular, the ovules numerous, attached to 4 vertical placental ridges, these axile in 2-locular ovaries and parietal in unilocular ovaries (a single placental ridge in each locule in some species of *Schlegelia*), style slender, stigma bilamellate; a nectariferous disc usually conspicuous, sometimes lacking. *Fruit* a capsule with dehiscence perpendicular or parallel to the septum or a berry or hard-shelled pepo (calabash); seeds without endosperm, somewhat flattened, usually winged, the cotyledons foliaceous.

A family of about 120 genera and 650 species, mostly tropical with a few genera in warm temperate regions. The family is divided into three major tribes and several minor ones. The Crescentieae and Tecomeae are found in both the Old and New Worlds. The Bignonieae *sensu stricto* are restricted to the New World. In Panama 35 genera and 75 species occur naturally, and an additional 7 genera and 11 species occur in cultivation.

The family is predominantly woody and includes several genera of large trees and many lianas. Opposite, compound leaves characterize the great majority of species of the family. The bud scales, termed pseudostipules, are often conspicu-

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[1] Assisted by National Science Foundation Grant GB-5674 (Thomas B. Croat, principal investigator).

[2] Assisted by a National Science Foundation graduate fellowship and pre-doctoral dissertation improvement grant.

[3] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 60: 781–977. 1973.

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ous and provide useful taxonomic characters. Presence or absence of concentrations of peltate glands into glandular fields at the nodes (interpetiolar glandular fields) or, less commonly, at the apex of the petiole (petiolar glandular fields) is another taxonomically useful character. However, glandular fields disappear on older branchlets and in some species may be either present or absent, so the character must be used with caution. The flowers are variously pollinated by bees, birds, butterflies, moths, or bats. Seeds are mostly wind-dispersed, but some are dispersed by water or by mammals.

The major economic importance of the family is in horticulture with many species widely cultivated for their showy flowers. A number of species of Tecomeae are important timber trees. The hard shells of the fruits of *Crescentia* are widely employed as household utensils.

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a. Herbaceous vines; inflorescence subspicate, the upper flowers mostly sterile; ovary 4-locular; capsule densely uncinate-spiny, bur-like, the valves not splitting to the base ---------- 40. *Tourrettia*

aa. Woody lianas or trees; inflorescence never spicate, without sterile flowers; ovary 1–2-locular, capsule not spiny with uncinate barbs, or if spiny not bur-like and the 2 valves completely dehiscent.

b. Trees or shrubs (*Podranea* and *Tecomaria*, both cultivated, are often vines); leaves various but not 2-foliolate and never tendrillate; stems without phloem arms in cross section; fruits dehiscing perpendicular to the septum or indehiscent and more than 7 cm long.

c. Leaves pinnately compound.

d. Leaves bipinnate, flowers purplish-blue; staminode longer than fertile stamens ---------- 15. *Jacaranda*

dd. Leaves once compound; flowers not bluish; staminode much shorter than fertile stamens.

e. Shrubs, vines, or small trees; corolla small (less than 6 cm long and 2 cm wide), tubular-infundibuliform to tubular-campanulate; native or exotic species.

f. Usually vines; flowers pink to lavender; calyx more than 1.0 cm long; cultivated ---------- 29. *Podranea*

ff. Usually trees or shrubs; flowers yellow to orange-red; calyx less than 0.8 cm long; cultivated or native.

g. Stamens included; flowers yellow; native shrub or small tree ..... 38. *Tecoma*

gg. Stamens exserted; flowers orange-red; exotic shrub or vine ..... 39. *Tecomaria*

ee. Trees; corolla large (more than 7 cm long and 4 cm wide), broadly campanulate; exotic species.

h. Calyx spathaceous; corolla red-orange; fruit a glabrous capsule ..... 34. *Spathodea*

hh. Calyx cupular, irregularly 2–5-lobed; corolla yellow or brownish maroon; fruit indehiscent or a pubescent capsule.

i. Corolla yellow, strongly pubescent; fruit dehiscent.. 14. *Haplophragma*

ii. Corolla brownish-maroon, glabrous; fruit indehiscent..... 16. *Kigelia*

cc. Leaves simple, 3-foliolate, or palmately compound.

j. Leaves alternate, opposite, or fasciculate; corolla thick, usually with a transverse fold in throat, whitish or greenish; the flowers borne singly or in fascicles (bat pollination syndrome), fruit indehiscent, fibrous-fleshy, or pulpy with a hard shell.

k. Leaves 3-foliolate, opposite; calyx spathaceously split (see also *Dendrosicus spathicalyx*); fruits without hard shell ..... 25. *Parmentiera*

kk. Leaves mostly simple, alternate or fasciculate (if compound then fasciculate in clusters); calyx not spathaceous (except in *D. spathicalyx*); fruits with hard shell (calabash).

l. Leaves alternate; placentation axile, at least at extreme base of ovary, above parietal on two placentae; seeds large (greater than 13 × 16 mm) ..... 11. *Dendrosicus*

ll. Leaves fasciculate; placentation parietal on four placentae; seeds small (less than 8 × 6 mm) ..... 8. *Crescentia*

jj. Leaves opposite; corolla thin, without transverse fold in throat, color various; inflorescence a raceme or panicle or reduced to a few flowers; fruit a dehiscent capsule.

m. Flowers less than 1.8 cm long; anthers pilose; fruits spirally twisted; leaflets 7–9, often cuneate to the base ..... 13. *Godmania*

mm. Flowers more than 2 cm long; anthers glabrous; fruits more or less straight; leaflets (1–)3–7, conspicuously petiolulate (unless 3-foliolate) ..... 36. *Tabebuia*

bb. Lianas, sometimes shrubby when young (see also *Podranea* and *Tecomaria*); leaves various but often 2-foliolate and usually in part tendrillate; stems (except *Schlegelia*) with 4–16 phloem arms in cross section; fruits dehiscing parallel to the septum or indehiscent and less than 4 cm long.

n. Leaves simple, tendrils lacking; placentation axile with a single central placenta in each locule, sometimes parietal with two bifid placentae toward top of ovary; fruit spherical, indehiscent ..... 32. *Schlegelia*

nn. Leaves usually compound, tendrils often present; placentation axile with 2 placentae in each locule; fruit more or less elongate or flattened, dehiscent.

o. Branchlets strongly 6-sided, the angles ribbed.

p. Tendrils apically 3-forked; leaves with dendroid trichomes; calyx double; corolla conspicuously bilabiate, the upper 2 and lower 3 lobes fused at anthesis ..... 2. *Amphilophium*

pp. Tendrils apically 3–15-forked; trichomes all simple; calyx simple; corolla slightly bilabiate, the lobes separate, subequal, reflexed at maturity ..... 27. *Pithecoctenium*

oo. Branchlets terete to tetragonal, not 6-ribbed.

q. Leaves 2–3-ternate; branchlets acutely tetragonal and the tendril trifid .... 28. *Pleonotoma*

qq. Leaves 2–5-foliolate (sometimes simple in part); branchlets various, if acutely tetragonal the tendril simple.

r. Corolla split about half its length, white; margins of capsule valves sharply raised; vegetative parts with odor of cloves ..... 41. *Tynnanthus*

rr. Corolla only slightly bilabiate, color various; margins of capsule valves not sharply raised; without odor of cloves.

s. Corolla orange, lobes valvate in bud; exotic ..... 30. *Pyrostegia*

ss. Corolla not orange, lobes imbricate in bud; native or exotic.

t. Branchlets conspicuously hollow; fruit narrow (less than 7 mm wide); leaves punctate ..... 35. *Stizophyllum*

tt. Branchlets not hollow; fruit more than 8 mm wide; leaves not punctate.

u. Tendrils uncinate-trifid with claw-like tips; flowers yellow; stem irregularly many-armed in cross section.

v. Calyx with a recurved apicule; capsule valves oblong, woody, splitting in half at maturity ..... 20. *Melloa*

vv. Calyx apicule wanting or incurved; capsule valves linear, not woody, not splitting in half ..... 18. *Macfadyena*

uu. Tendrils simple or trifid without claw-like tips; flowers lavender, white, or yellow; stem symmetrically 4–16-armed in cross section.

w. Leaves ± dendroid-pubescent, at least in vein axils beneath; capsule oblong, the valves woody, compressed, smooth, the seeds thin with broad wings.

x. Interpetiolar glandular fields present; calyx small (less than 9 × 5 mm); corolla lavender; seed wings hyaline ..... 42. *Xylophragma*

xx. Interpetiolar glandular fields absent; calyx large (greater than 22 × 22 mm); corolla yellow; seed wings brown ..... 5. *Callichlamys*

ww. Leaf pubescence of simple trichomes or lepidote scales or wanting; capsule various but without above combination of characters.

y. Calyx with narrow, elongate (to 5 mm), twisted teeth; capsule oblong, conspicuously large tuberculate ..... 22. *Onohualcoa*

yy. Calyx various but marginal teeth lacking or less than 1 mm long; capsule oblong or linear, not large-tuberculate.

z. Anthers pubescent (see also *Pachyptera kerere* and *Cuspidaria floribunda*, these with curved anther thecae and obvious disc), the thecae straight; disc absent; capsule pubescent, the midrib and margins raised ..... 17. *Lundia*

zz. Anthers mostly glabrous (pubescent in some species of *Pachyptera* and *Cuspidaria*); thecae straight or curved; disc present or absent; capsule glabrous or lepidote, if pubescent then evenly flattened.

A. Flowers yellow, sometimes with reddish splotches (*Mussatia*), or white (see also *Cydista aequinoctialis* and *Arrabidaea* spp.); disc present; capsule valves more or less woody, more than 2.5 cm wide, not echinate.

B. Twigs sharply tetragonal, the angles ribbed; corolla small, less than 2 cm long; calyx shallowly campanulate, less than 2 mm long ..... 21. *Mussatia*

BB. Twigs subterete to subtetragonal, without conspicuous angles; corolla more than 2.5 cm long; calyx cupular, more than 5 mm long.

C. Capsule stipitate, orbicular or elliptic; ovary usually stipitate; corolla glabrous (see also *Tanaecium nocturnum* with white flowers) or lepidote, cream or yellow, not white ..... 3. *Anemopaegma*

CC. Capsule ± oblong; ovary not stipitate; corolla pubescent outside (except *Tanaecium nocturnum*), cream, yellow or white.

D. Leaves with petiolar glandular fields; pseudostipules vertically 3-seriate (see Fig. 23C, page 891) ..... 23. *Pachyptera*

DD. Leaves without petiolar glandular fields; pseudostipules not vertically 3-seriate.

E. Tendril trifid.

F. Capsule ± flattened, wider than thick, basally rounded; interpetiolar glandular fields lacking ..... 12. *Distictella*

FF. Capsule subtetragonal, basally gibbous; interpetiolar glandular fields present ..... 6. *Ceratophytum*

EE. Tendril simple.

G. Leaves with almond (cyanide) odor, never with cartilaginous margin; corolla elongate-tubular, salverform, white.. 37. *Tanaecium*

GG. Leaves without almond odor, usually with at least traces of a cartilaginous margins; corolla tubular-campanulate or tubular-infundibuliform, yellow ..... 1. *Adenocalymma*

AA. Flowers magenta to lavender (some species have white-flowered forms); disc present or absent; capsule valves not woody unless echinate, mostly less than 2.5 cm wide.

H. Calyx spathaceous; surface of capsule valves gray, densely lepidote, appearing rough-crystalline under a lens ..... 26. *Phryganocydia*

HH. Calyx not spathaceous; surface of capsule valves rarely gray, not rough-crystalline under a lens.

I. Capsule suborbicular, echinate; pseudostipules clusters of cataphylls resembling miniature bromeliads, most conspicuous at base of inflorescence..... 7. *Clytostoma*

II. Capsule linear (rarely linear-oblong), not echinate (sometimes verrucose); pseudostipules not clusters of cataphylls, the inflorescence without cataphylls at base.

J. Plant with strong onion odor (except *P. parvifolia* with disc-tipped tendrils); tendril trifid or ending in a peltate disc; mature capsule drying straw-colored or light brown, smooth, more than 1.7 cm wide, the margins not raised; petiolar and interpetiolar glandular fields often present.... 23. *Pachyptera*

JJ. Plant without onion odor; tendrils simple or trifid, never ending in a peltate disc; mature capsule usually drying blackish to brownish, verrucose to sandpaper-surfaced or smooth, less than 2 cm wide (except in *Cydista aequinoctialis* with raised margins), the margins raised or not; petiolar glandular fields only in *Paragonia* with simple or minutely bifid tendrils; interpetiolar glandular fields only in *Arrabidaea* and *Scobinaria* both with simple tendrils.

phylla) ..... 19. *Martinella*

K. Tendril conspicuously trifid; fruit more than 55 cm long, uniformly flat, glabrous; inflorescence a raceme (see also *Cydista hetero-*

KK. Tendril simple or minutely bifid; fruit less than 60 cm long, compressed but with edges raised or sharply angled or the midline thicker, glabrous or pubescent inflorescence usually a panicle (a raceme in *Cydista heterophylla*).

L. Calyx large (more than 18 mm long) and bilabiate; capsule verrucose ..... 33. *Scobinaria*

LL. Calyx less than 9 mm long, usually more or less truncate; capsule not verrucose.

M. Corolla glabrous outside; leaflets basally attenuate; pseudostipules foliaceous on terete branchlets; cultivated ..... 31. *Saritaea*

MM. Corolla puberulous or lepidote outside at least on lobes; leaflets basally rounded to broadly cuneate; pseudostipules only foliaceous if early deciduous or on sharply tetragonal branchlets; native.

N. Disc wanting; interpetiolar glands absent; stems with 8–16 phloem arms in cross section; branchlets sometimes tetragonal ..... 10 *Cydista*

NN. Disc present, obvious; interpetiolar glands often present; stems with 4 phloem arms in cross section; branchlets not tetragonal.

O. Leaflets elliptic, drying gray, with faint sweet odor when fresh; pseudostipules appressed-conical; tendril usually minutely bifid; capsule valves convex, rough ..... 24. *Paragonia*

OO. Leaflets ovate to elliptic or round, not drying gray, without sweet odor when fresh; pseudostipules inconspicuous or wanting; tendril simple; capsule valves not convex and rough-surfaced.

P. Capsule valves with raised lines bordering a median furrow; anther thecae strongly reflexed, pollen in tetrads ..... 9. *Cuspidaria*

PP. Capsule valves uniformly flattened, or the median nerve and/or margins slightly raised; anther thecae straight or slightly bent, pollen grains single ..... 4. *Arrabidaea*

1. ADENOCALYMMA

Adenocalymma Mart. *ex* Meisn., Gen. 1: 300; 2: 208. 1840. LECTOTYPE: *A. comosum* (Cham.) DC.

Lianas; stems with 4 phloem arms in cross section; branchlets terete, without interpetiolar glandular fields, pseudostipules small, more or less subulate, not foliaceous. *Leaves* 3-foliolate, the terminal leaflet often replaced by a simple tendril. *Inflorescence* a narrow axillary or terminal bracteate raceme, each bud subtended by a caducous glandular bract. *Flowers* with the calyx cupular, bilabiate to more or less truncate, usually with conspicuous plate-shaped glands in upper part; corolla yellow, tubular-infundibuliform to tubular-campanulate, usually pubescent outside; anthers glabrous, the thecae straight, divaricate or somewhat divergent; pollen ecolpate, the exine alveolate; ovary narrowly cylindrical, lepidote or puberulent, the ovules 2-seriate in each locule; disc pulvinate. *Fruit* an oblong capsule, the valves parallel to the septum, only slightly compressed, woody, usually with more or less raised lenticels, the median nerve not conspicu-

ous; seeds bialate or almost wingless, the body thick and corky, the wings when present poorly demarcated, brown at the base and hyaline toward the ends.

a. Leaves ovate, drying shiny gray with a distinct cartilaginous margin; twigs usually drying dark with pale flecks; corolla tubular-infundibuliform; anther thecae slightly divergent, the connective apiculate ..... 1. *A. apurense*
aa. Leaves narrowly ovate, drying gray-green without a distinct cartilaginous margin; twigs drying tannish; corolla tubular-campanulate; anther thecae widely divaricate, the connective not extended ..... 2. *A. arthropetiolatum*

1. **Adenocalymma apurense** (H.B.K.) Sandw., Lilloa 3: 461. 1938.—Fig. 1A–D.

Bignonia apurensis H.B.K., Nov. Gen. Sp. Pl. 3: 138. 1819. TYPE: Venezuela, Río Apure, *Humboldt & Bonpland 812* (P).
Adenocalymma inundatum Mart. *ex* DC., Prodr. 9: 201. 1845. TYPE: Brazil, Pará, *Martius s.n.* (1819) (M).
A. grenadense Urb., Fedde Repert. 14: 306. 1916. TYPE: Grenada, prope Belmont, *Broadway 1798* (C, GH, M, NY).
Tabebuia calderonii Standl., Jour. Washington Acad. Sci. 14: 244. 1924. TYPE: El Salvador, Sonsonate, *Calderon 1666* (US).
Adenocalymma hintonii Sandw., Kew Bull. 1936: 10. 1936. SYNTYPES: Mexico, México, *Hinton 3784* (K, MO); Guerrero, *Hinton 7259* (K, MO, US).
A. calderonii (Standl.) Seib., Carnegie Inst. Washington Publ. 522: 428. 1940.

Liana to 10 cm in diameter, the bark smooth, gray, often 4-furrowed; twigs subterete, glabrous to slightly lepidote, usually drying black with whitish lenticels when young; pseudostipules small, pointed, usually ± ovate. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate to elliptic ovate, acute to acuminate, basally rounded, truncate or almost subcordate, 4.5–17 cm long and 2.2–8.8 cm wide, membranaceous to chartaceous, secondary veins 5–7 on a side, the nerve axils beneath with inconspicuous glandular fields, somewhat lepidote, at least beneath, usually puberulous at base of midvein above, drying shiny dark gray or dark olive with a conspicuous narrow cartilaginous margin; tendril simple, 4–13 cm long; petiolules 0.9–4 cm long, petioles 3.2–6.5 cm long, petiole and petiolules flattened above, inconspicuously lepidote, slightly puberulous above at least at base and apex. *Inflorescence* an axillary raceme, an enclosing deciduous bract ca. 1 cm long and 1 cm wide with conspicuous sunken glands subtending each bud, the rachis and pedicels puberulous. *Flowers* with the calyx cupular, minutely 5-toothed but bilabiately split for 1–2 mm, 5–8 mm long and 4–6 mm wide, puberulous, usually with plate-shaped glands; corolla bright yellow, 2.5–6.9 cm long and 0.9–1.9 cm wide at the mouth, the base cylindric, 6–7 mm long and 4–5 mm wide above, infundibuliform-campanulate, the tube often bent somewhat anteriorly, 1.8–5.0 cm long, the lobes all ± reflexed, 1.0–2.0 cm long; puberulous outside with simple and thick-stellate trichomes, glandular-lepidote inside on the lobes and sparsely so in the tube, with longer 1–2-celled trichomes at the level of stamen insertion; stamens didynamous, included, the anther thecae slightly divergent, slender, 2–3 mm long, the connective with a 1 mm apicule, the longer filaments 1.4–1.7 cm long, the shorter filaments 0.9–1.3 cm long, staminode 4–5 mm long, inserted 4–7 mm from the base of the corolla tube; pistil 2.4–2.5 cm long, ovary cylindric, 3–3.5 mm long and 1.5–2 mm wide, lepidote, the ovules 2-seriate, disc pulvinate, 2 mm long and 3 mm wide. *Capsule* oblong, rounded at both ends, not compressed, the valves woody and somewhat thickened, the midrib

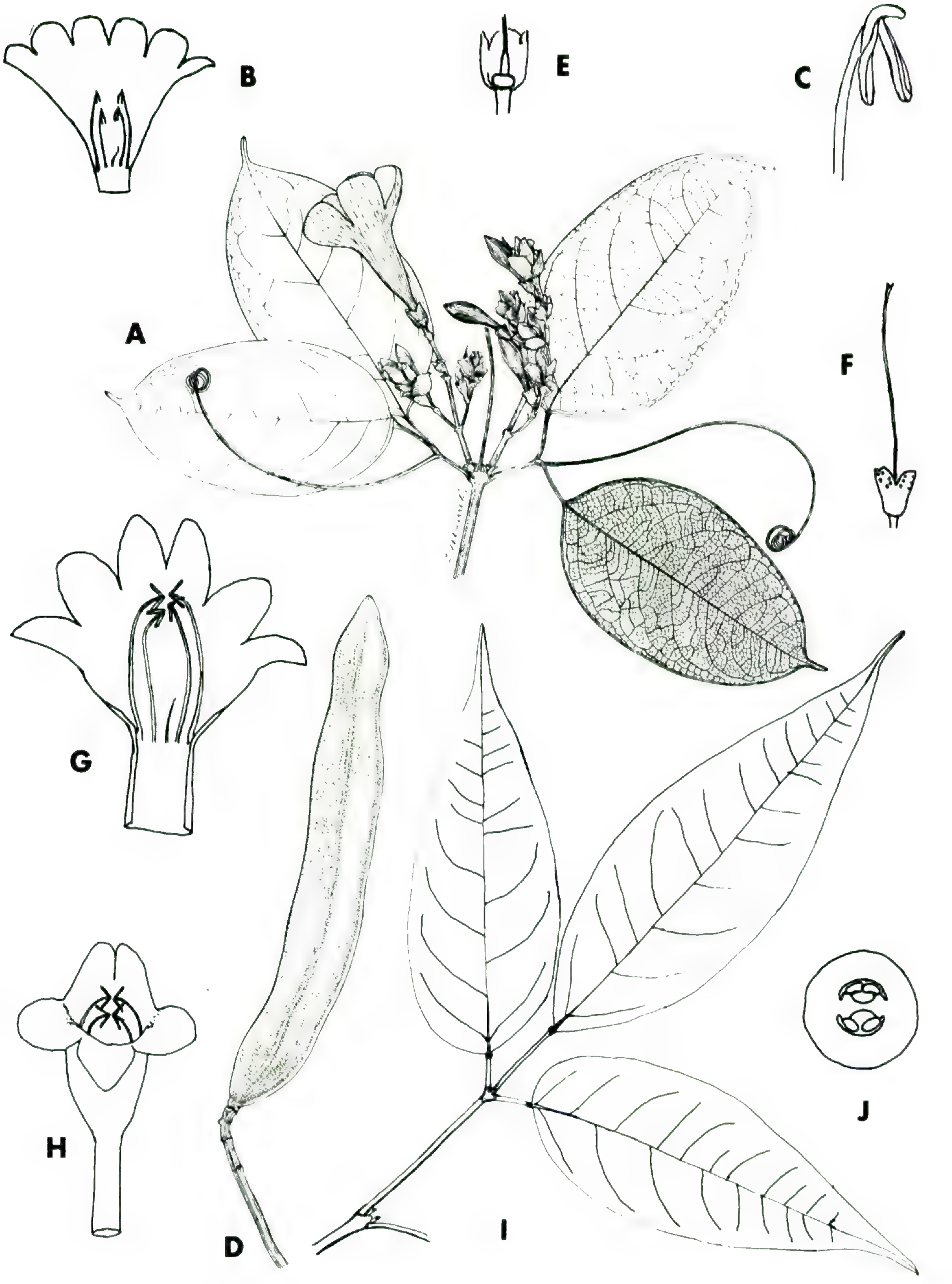

FIGURE 1. *Adenocalymma*.—A–D. *A. apurense* (H.B.K.) Sandw.—A. Habit (× 3/8). [After *Woodson et al. 1578* (MO).]—B. Corolla split open (× ½).—C. Anther (× 5). [After *Gentry & Tyson 5023* (MO).]—D. Fruit (× 3/10). [After *Hinton 7259*, Mexico (MO).]—E–J. *A. arthropetiolatum* A. Gentry.—E. Ovary and disc (× ½).—F. Calyx and pistil (× ½).—G. Corolla split open (× ½).—H. Corolla (× ½).—I. Leaf (× ½).—J. Ovary cross section (× 9). [After *Gentry 2460* (MO).]

obscure, 9.5–27 cm long and 2.5–3.1 cm wide, 1.4–2.2 cm thick, glabrous but rough-surfaced, gray with numerous raised tan lenticels; seeds 1.7–2.1 cm long and 5.1–7.6 cm wide, the body thick and corky, the wings thin, brown and membranaceous, subhyaline to hyaline at tips and not sharply demarcated.

A vine of the tropical dry forest and edaphically dry regions of the tropical moist forest, this species is known only from riverine gallery forests over much of its range; from Mexico to the Guianas. Flowering mostly during the late dry season and early wet season from mid-April through August, it has also been collected in flower in February. Although the heavy-bodied seeds have wings, they are probably water dispersed at least in part. This may account for mature plants occurring almost invariably adjacent to streams.

The ovate leaflets of this species are useful characters for differentiating it from *A. arthropetiolatum*, which has narrowly ovate leaflets. The included anthers with slightly divergent thecae separate the flowers from those of *A. arthropetiolatum*.

This species has in the past been well known from Mexico to El Salvador as *A. calderonii* (Standl.) Seib. or *A. hintonii* Sandw. and in northern South America as *A. inundatum* Mart. *ex* DC. In large part because of the seeming disjunction across most of Central America, Sandwith (Kew Bull. 1953: 481. 1954) maintained the two as separate species. However collections from Costa Rica and Panama close the range gap and re-examination of the minor characters purporting to separate the two species disclosed that they are the same. The name *A. apurense* (H.B.K.) Sandw. has priority over either of the names in current use.

CANAL ZONE: Salamanca Hydrographic Station, *Woodson et al. 1577, 1578* (both A, MO, NY). CHIRIQUÍ: 7.5 mi. W of Puerto Armuelles *Croat 22471* (MO). Near Puerto Armuelles, *Woodson & Schery 809* (GH, MO, US). DARIÉN: Río Chucunaque between Ríos Membrillo and Subcuti, *Duke 8607* (MO). Punta Patiño NNE of Garachiné, *Gentry 4044* (MO). Río Chucunaque above Río Tuquesa, *Stern et al. 946* (G, GH, K, MO, US). LOS SANTOS: Guánico near Tonosí, *Stern et al. 1850* (MO, US). PANAMÁ: Near Madden Lake, *Gentry 5023* (MO).

2. **Adenocalymma arthropetiolatum** A. Gentry.[4] TYPE: Panama, Canal Zone, Pipeline Road, *Gentry 2460* (MO).—FIG. 1E–J.

Liana to 3 cm in diameter, the bark smooth, greenish, with inconspicuous lenticels; branchlets subterete to subtetragonal, glabrous to subscabrous, drying tan to greenish, pseudo-stipules small, 4-scaled, usually narrow. *Leaves* 3-folioate or 2-foliolate with a tendril or tendril scar; leaflets drying olive, narrowly ovate to almost linear, acute, basally truncate, 5.2–17 cm long and 1.9–7.5 cm wide, ± chartaceous, secondary veins 5–7 on each side, above scabrous along the midvein, beneath almost glabrous or puberulous along main veins and sometimes sparsely

[4] *Adenocalymma arthropetiolatum* A. Gentry, sp. nov. Frutex scandens, cortice laevi, viridi; ramuli subteretes, sine consociebus glandularum in nodis inter petioles; pseudostipulae parvae; folia bifoliolata vel trifoliolata, saepe cirrata simplici cirrho, foliolis anguste ovatis; inflorescentia floribus in racemis axillaribus dispositis, unoquisque flore per bracteam glandulosam caducam subtento; calyx cupulatus, 5-dentatus sed leviter bilabiatus, puberulus; corolla aurata, campanulata super basem tubularem; stamina subexserta, thecis glabris, divaricatis; ovarium anguste cylindricum, puberulum, ovulis in quoque loculo biseriatis; discus cupulatus-pulvinatus; capsula ignota.

on the surface, with a few scattered plate-shaped glands; tendril simple, to 14 cm long; petiolules 0.5–4.1 cm long, the petiole 1.1–6.4 cm long, puberulous, woody proximally and conspicuously jointed with the petiolules. *Inflorescence* an axillary or terminal raceme, a subtending glandular, deciduous bract enclosing each bud, the rachis and pedicels puberulous. *Flowers* with a faint musky odor, the calyx cupular, 5-toothed but more or less bilabiate, 5–15 cm long and 4–10 mm wide, puberulous with simple and thick-stellate trichomes, usually with conspicuous submarginal sunken cupular glands; corolla uniformly bright yellow, often a slightly deeper shade within, campanulate, 4.2–8.2 cm long and 1.1–2.1 cm wide at the mouth, the base cylindrical, 2.3–2.6 cm long and 0.6–0.7 cm wide, the tube 2.5–5.6 cm long, the lobes often folded or rolled, the upper shorter two lobes 1.2–1.7 cm long, extending horizontally in front of the tube, the longer three lobes 1.8–2.3 cm long, variously reflexed, outside and inside the lobes puberulent with simple and thick-stellate trichomes, the tube glabrous inside except for slender 2–3-celled gland-tipped trichomes at and just below the level of stamen insertion, the base of the lobes with plate-shaped glands outside; stamens slightly exserted, the anthers held underneath the hood formed by 2 projecting upper corolla lobes, the anther thecae more or less divergent, 5–6 mm long, the filaments more or less equal, the anterior pair 3.5–3.9 cm long, the posterior pair 3.3–4.0 cm long, the staminode 12–21 mm long, inserted 2.1–2.6 mm from base of corolla tube, pistil 5.0–5.9 cm long, the ovary narrowly cylindrical, 4–5 mm long and 1.5–2.0 mm wide, puberulent, the ovules 2-seriate; disc pulvinar-cupulate, 1.5–2.5 mm long, 4–6 mm wide. *Capsule* unknown.

Apparently restricted to stream banks and lake shores of the tropical moist forest and premontane wet forest of central Panama, this plant flowers during the late wet season in October and November and is thus temporally isolated from its congener *A. apurense*.

The smooth greenish bark and wiry, strongly bent petiole and petiolule joints are distinctive. Narrowly ovate leaflets which are slightly 3-nerved at the base also aid in distinguishing it from *A. apurense*.

This species is most closely related to *A. magdalenense* Dugand of the Magdalena Valley of Colombia, which is vegetatively distinguishable mainly by its much larger, glandular, subfoliaceous pseudostipules. The corolla of *A. magdalenense*, however, is evenly and narrowly tubular-infundibuliform with strongly exserted anthers as opposed to *A. arthropetiolatum* which has its corolla abruptly tubular-campanulate above a narrowly tubular base and subexserted anthers held under a hood formed by the forward-projecting upper corolla lobes.

Adenocalymma arthropetiolatum is unusual in the family and especially in the Bignonieae in its restricted geographical range. Since all collections of this species have come from along rivers or lakes, the seeds, when discovered, may prove to be water dispersed. Probably because of this it is restricted to the drainages of the Ríos Bayano and Chagres plus the adjacent Ríos Pasiga and Maestro.

CANAL ZONE: Pipeline Road, *Gentry 1435, 2460* (both MO); Barro Colorado Island, *Standley 40912* (US). PANAMÁ: Río Aguacate near El Llano, *Duke 5828* (MO, SCZ). Near mouth of Río Pasiga, *Gentry 2205A* (MO). Río Maestro, *Gentry 2240* (MO). Río Piragua

(Tabardí), *Gentry 2519* (MO). Between Ríos Espavé and Agua Clara, *Gentry 3772* (MO). Near Madden Lake, *Gentry 5011* (MO).

2. AMPHILOPHIUM

Amphilophium Kunth, Jour. Phys. Chim. Hist. Nat. Arts 87: 451. 1818. LECTOTYPE: *A. paniculatum* (L.) H.B.K.

Endoloma Raf., Sylva Tell. 79. 1838. TYPE: *E. purpurea* Raf. = *Amphilophium paniculatum* (L.) H.B.K.

Lianas, stems with 4(–5) phloem arms in cross section; branchlets sharply hexagonal with conspicuous ribs, without interpetiolar glandular fields; pseudostipules foliaceous, often early deciduous. *Leaves* 2–3-foliolate, the terminal leaflet often replaced by a trifid tendril. *Inflorescence* a terminal racemose panicle usually on a short lateral branch. *Flowers* with the calyx campanulate, double, with a thick inner tube and a spreading, frilly outer limb; corolla purple at maturity, thick, tubular, bilabiate, split about half its length and the upper 2 lobes and lower 3 lobes fused, glabrous or somewhat pubescent outside; anthers glabrous, the thecae thick, divaricate; pollen grains single, 6–8-colpate, the exine alveolate; ovary ovate-cylindric, the ovules multiseriate in each locule. *Fruit* an oblong-elliptic capsule, the valves parallel to the septum, somewhat compressed, woody, smooth to tuberculate; seeds thin, puberulous winged, the wings membranaceous, brownish to hyaline at tip and not sharply demarcated from the seed body.

About 5 species ranging from Mexico and the West Indies throughout tropical America to northern Argentina.

a. Pseudostipules persistent and conspicuous; capsule compressed, rugose-tuberculate; vegetative parts with pronounced pubescence, at least partially of long (1–2 mm) trichomes; tropical wet forest ..... 2. *A. pannosum*
aa. Pseudostipules early caducous; capsule only slightly flattened, smooth or rugose-wrinkled; vegetative parts lepidote to variously short pubescent with mostly dendroid trichomes; throughout Panama ..... 1. *A. paniculatum*

1. **Amphilophium paniculatum** (L.) H.B.K., Nov. Gen. Sp. Pl. 3: 116. 1819. —FIG. 2.

Bignonia paniculata L., Sp. Pl. 623. 1753. TYPE: (not seen).
Amphilophium macrophyllum H.B.K., Nov. Gen. Sp. Pl. 3: 150. 1819. TYPE: Colombia, near Turbaco, *Bonpland s.n.* (F, fragment).
A. mutisii H.B.K., Nov. Gen. Sp. Pl. 3: 149, *tab. 219*. 1819. TYPE: Colombia, *Mutis 913* (US).
A. molle Schlecht. & Cham., Linnaea 5: 120. 1830. TYPE: Mexico, Veracruz, *Schiede & Deppe s.n.* (not seen).
Endoloma purpurea Raf., Sylva Tell. 80. 1838. (nom. nov. for *Bignonia paniculata* L.).
Amphilophium vauthieri DC., Prodr. 9: 193. 1845. TYPE: Brazil, Rio de Janeiro, *Vauthier 249* (G-DC, P; F, fragment).
A. xerophilum Pittier, Jour. Washington Acad. Sci. 18: 121. 1928. TYPE: Venezuela, Lara, *Sauer 253* (K).
A. paniculatum var. *molle* (Schlecht. & Cham.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1114. 1938.

Liana to at least 10 cm in diameter, the bark loose, fibrous, vertically striate; stem with 4(–5) arms in cross section; branchlets sharply hexagonal with ribbed

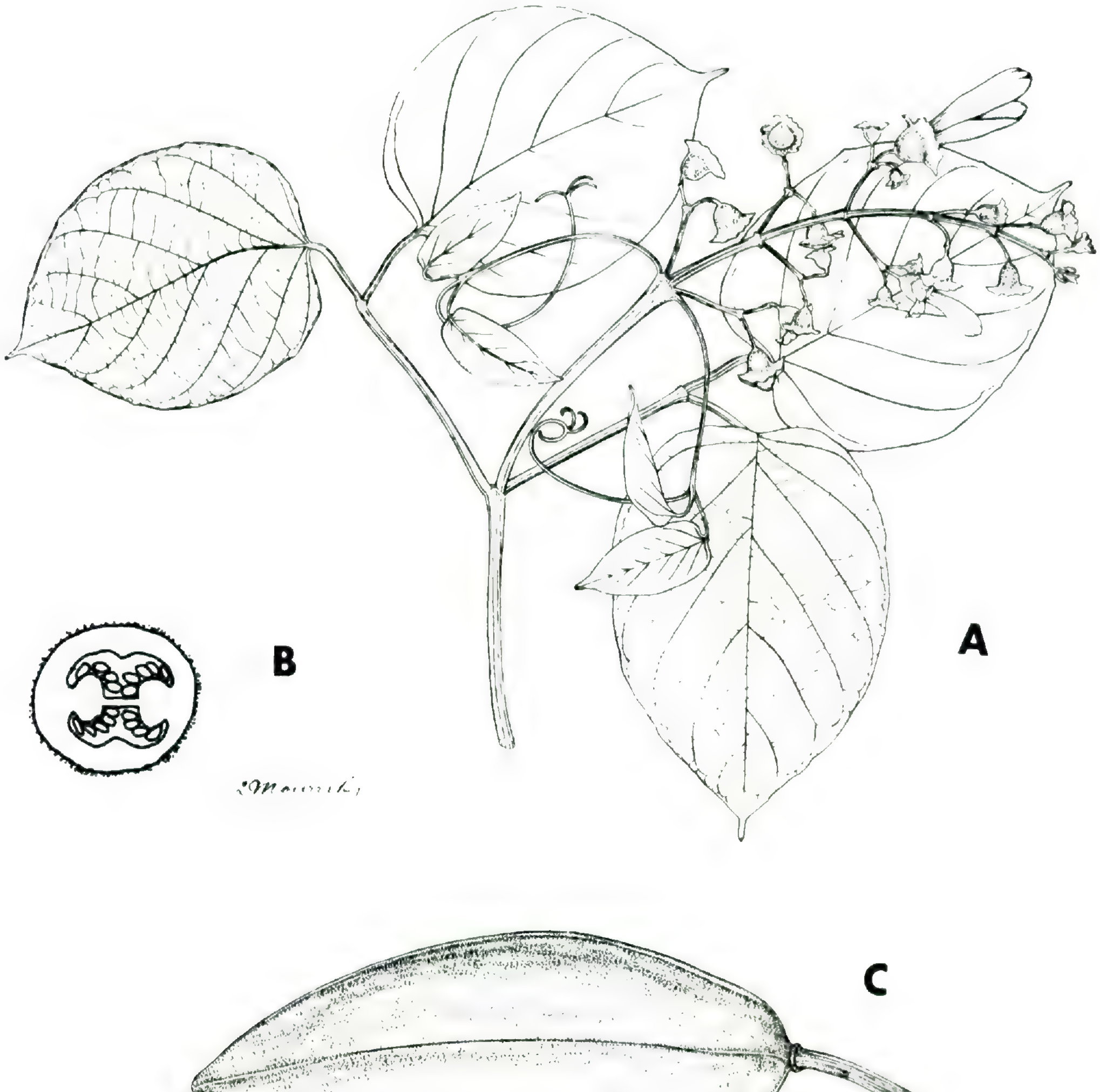

FIGURE 2. *Amphilophium paniculatum* (L.) H.B.K.—A. Habit (× 3/5). [After *Gentry 3120* (MO).]—B. Ovary cross section (× 9).—C. Fruit (× 3/5). [After *Allen 205* (MO).]—D. Pistil and disc (× 3/5).—E. Flower in dorsal and ventral view (× 3/5).—F. Corolla slit open (× 3/5). [After miscellaneous fresh material.]

angles, lepidote to strongly dendroid pubescent, especially on the ribs, interpetiolar glandular fields lacking, a conspicuous ridge connecting opposite petioles; pseudostipules foliaceous, 3–10 mm long and 3–6 mm wide, early deciduous. *Leaves* 2-foliolate except on young plants, sometimes with a tendril; leaflets ovate to subrotund, acuminate to obtuse, truncate to asymmetrically cordate, 2.5–16 cm long and 2.1–10.7 cm wide, membranaceous, palmately veined at base, the secondary veins 4–6 on a side, strongly lepidote above and beneath, variably dendroid pubescent, sometimes also with simple trichomes especially above, pubescence beneath restricted to midveins and nerve axils or scattered throughout, gray to brown when dry, lighter beneath; tendril trifid, 7–16 cm long to branching, the 3 arms 0.4–2.5 cm long, often unequal; petiolules 0.6–4.3 cm long; petiole 2.3–7.1 cm long; petiole, petiolules, and tendril all ± tetragonal to hexagonal, lepidote and dendroid pubescent. *Inflorescence* a caducously bracteate ± racemose terminal panicle on a short erect lateral branch, the branches lepidote and variably dendroid pubescent. *Flowers* with some odor, calyx double, the inner calyx 2–3-labiate, the outer calyx more or less 5-lipped, densely lepidote, sometimes dendroid pubescent, especially at the base, 0.7–1.2 cm long and 0.8–1.5 cm wide; corolla yellowish white when young, turning deep purple, tubular, bilabiate, 2.4–3.5 cm long and 0.7–1.6 cm wide, the upper 2 lobes fused, thick, 1 mm long, the lower 3 fused, 1.3–1.8 cm long, the tube split ⅓–⅔ its length, all 5 lobes remaining loosely fused until forced apart by pollinator, viscid, glabrous to sparsely short simple pubescent outside, inside mostly glabrous, glandular-lepidote on the ridge at the level of stamen insertion, below this the epidermis highly convoluted and glandular; stamens didynamous, the anther thecae divaricate, 2 mm long, the longer filaments 1.7–1.8 cm long, the shorter filaments 1.4–1.5 cm long, the staminode 3–5 mm long, inserted 4–5 mm from base of corolla tube; pistil 2.4–2.7 cm long, bent 0.7–0.8 cm from the base, the ovary ovate-cylindric, slightly contracted at base, 2–3 mm long, ca. 2 mm wide, short pubescent with simple and dendroid trichomes, the ovules more or less 10-seriate in each locule below to only 4-seriate distally; disc annular-pulvinate, 1 mm long, 3–4 mm wide. *Capsule* rounded oblong, somewhat flattened, 3.9–9.5 cm long and 2.5–3.8 cm wide, 1.4–2 cm thick, the surface dark, somewhat warty-lenticellate, densely lepidote; seeds 1–1.9 cm long and 2.7–3.0 cm wide, puberulous, the wings membranaceous, brownish, not sharply demarcated, irregularly hyaline only at extreme tips.

Ecologically this is the most wide-ranging species of Central American Bignoniaceae, occurring in the lowland tropical dry, moist, and wet forests and also to 6000 feet in montane cloud forest. The higher elevation forms tend to be more pubescent and have been designated as *A. molle* or *A. paniculatum* var. *molle* in Central America. *Amphilophium macrophyllum* of northern South America is this same form. There is complete intergradation, and the variation in extent of pubescence is more or less clinal with elevation. The species ranges from Mexico and the West Indies to Argentina.

Amphilophium paniculatum flowers in the wet season and early dry season from May through January. The corolla is pseudocleistogamous, never opening completely. Its lobes are reduced to two lips which cover the tube and remain fused until forced apart; even after having been opened they are held strongly

together. The peculiar double calyx serves a dual purpose as well; the thick inner sleeve surrounds and protects the nectar-filled corolla base, while the outer sleeve even in bud secretes a sticky substance which attracts wasps, trigonids, and ants, the latter presumably forming an "ant guard" of the type typical for xylocopid-flowers. It possibly also acts as a scent attractant. Pollination is of necessity by robust bees. The flowers reach maximum size at least a day before anthesis but are yellowish white in color, turning purple with anthesis. Purple flowers are preferentially visited by pollinators, which enter by landing at the tip of the corolla, inserting their proboscis into the fusion line between the upper and lower lips, and pushing the lips apart with their head.

The most useful field character for recognition of this species is the hexagonal branchlet. The relatively short, ovate pseudostipules, tendrils never with more than three arms, and the presence of dendroid trichomes distinguish A. *paniculatum* from *Pithecoctenium echinatum*, which also has 6-sided twigs but elongate pseudostipules, up to 15-branched tendrils, and only simple trichomes.

BOCAS DEL TORO: Water Valley, *von Wedel 1749* (MO). CANAL ZONE: Near Cerro Viejo, *Blum 1258* (MO, SCZ). Venado Beach, *Correa 509* (MO, PMA, SCZ). Boy Scout Camp Road, *Gentry 1376* (MO). Pipeline Road, *Gentry 1434, 1579* (both MO); *Gentry & Dressler 1980* (MO). Curundu, *Gentry 1594* (MO). Highway K10, *Gentry 1959* (MO). Balboa, *Standley 26091* (MO). Sosa Hill, *Standley 26487* (GH, K). Curundu, *Tyson & Blum 2530* (MO, SCZ). Barro Colorado Island, *Aviles 22* (F); *Croat 4684, 9789* (both MO), *12499* (NY, SCZ), *12870* (MO); *Foster 1918* (GH, PMA); *Frost 213* (F). CHIRIQUÍ: W of Río Chorchita, *Gentry 5850* (MO). David airport, *Lewis et al. 760* (MO). Near Boquete, *Stern et al. 1144* (GH, K, MO). Cerro Punta, *Tyson 5821* (SCZ). COCLÉ: Río Grande, *Burch et al. 1164* (GH, MO). El Valle, *Gentry 3571* (MO); *Lewis et al. 2578* (MO, SCZ); *Pittier 5002* (NY). Río Grande, *Tyson 5243* (SCZ). COLÓN: Giral near Bat Cave, *Blum & Tyson 520* (MO, SCZ). Santa Rita Ridge, *Gentry 1432, 1881* (both MO). DARIÉN: Santa Fé, *Duke 14243* (MO). Isla Encanto, *Gentry 4021* (MO). 3–4 mi. S of Jaqué, *Gentry 4130* (MO). Río Jaqué, *Gentry 4201* (MO). El Real, *Gentry 4511* (MO). Cerro Pirre, *Gentry 4645* (MO). HERRERA: Río Santa María, *Burch et al. 1186* (GH, MO). Along main road between Ocú and Chitré, *D'Arcy & Croat 4146* (MO). S of Ocú, *Gentry 3120* (MO). E of Las Minas, *Gentry 3139* (MO). Santa María, *Seemann 153* (K). S of Pesé, *Tyson et al. 2885* (MO, SCZ). N of Macaracas, *Tyson et al. 3140* (MO, SCZ). LOS SANTOS: S of Chitré, *Burch et al. 1219* (F, GH, K, MO). PANAMÁ: Near Nueva Gorgona, *Duke 4533* (MO). Between Chepo and Río Mamoní, *Duke 6056* (MO). San José Island, *Erlanson 64* (GH, NY); *Johnston 422* (GH, MO), *644* (GH). S of Pacora, *Gentry 1412* (MO). Río Piragua (Tabardí), *Gentry 2531* (MO). Icantí (Río Agua Clara), *Gentry 2621* (MO, SCZ). Near Río Espavé, *Gentry 3725* (MO). Between Bayano crossing and Río Partí, *Gentry 3810* (MO). Cerro Campana, *Gentry 4925* (MO). Taboga Island, *Standley 27112* (GH). Juan Díaz, *Zetek 905* (F). SAN BLAS: Puerto Obaldía, *Gentry 1551* (MO). VERAGUAS: Trail between Cañazas and foot of Cordillera Central, headwaters of Río Cañazas, *Allen 205* (MO). Soná, *Allen 1064* (GH, MO). S of Santa Fé, *Gentry 2929, 2940* (both MO). Mountains above Santa Fé, *Gentry 2984, 3098* (both MO). Río Santa María S of San Francisco, *Gentry 3116* (MO). W of Santiago, *Tyson 5164* (SCZ).

2. **Amphilophium pannosum** (DC.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 209. 1896.

Bignonia pannosa DC., Prodr. 9: 148. 1845. TYPE: Peru, *Pavon s.n.* (F, fragment and photo).
B. pubescens Pav. *ex* DC., Prodr. 9: 148. 1845, pro syn, non L.
A. oxylophium Donn. Sm., Bot. Gaz. (Crawfordsville) 31: 119. 1901. TYPE: Costa Rica, Tucurrique, *Tonduz 13045* (MO, US).

Liana to at least 2.5 cm in diameter, branchlets sharply hexagonal with the angles ribbed, lepidote and strongly villous with long (to 2 mm) reddish yellow

trichomes, especially on ribs, these simple, forked and variously dendroid; interpetiolar glands lacking; pseudostipules foliaceous, 0.6–1.6 cm long and 0.6–1.4 cm wide, persistent. *Leaves* 3- or 2-foliolate with a tendril or tendril scar; leaflets ovate, acuminate, cordate to subcordate, 7.6–12.6 cm long and 5.4–8.8 cm wide, membranaceous, palmately veined at the base, the secondary veins 4–5 on each side, strongly lepidote above and beneath, villous above with simple or weakly dendroid trichomes and beneath with much branched dendroid trichomes, golden brown when dry; tendril trifid, 8–18 cm long to branching, the 3 arms 0.8–1.7 cm long, often recurved at the tip; petiolules 1.3–3.7 cm long, petiole 3.0–5.1 cm long, lepidote and villous. *Inflorescence* a terminal raceme on a short erect lateral branch, the branches lepidote and dendroid-villous, each flower subtended by a pair of narrow bracts below the calyx and a single bract below the pedicel. *Flower* with the calyx double, the inner calyx 2–3-labiate, the outer calyx more or less 5-lipped, 1.2–1.4 cm long and 1.2–1.9 cm wide, densely lepidote, densely dendroid-villous below the outer calyx lobes, sparsely so on them; corolla yellowish white when young, turning deep purple, tubular, 2.2–2.6 cm long and 0.6–0.9 cm wide, the upper 2 lobes fused and thick, 1 mm long, the lower 3 fused, 6–8 mm long, the tube bilabiate, split about half its length, the 2 lips remaining loosely fused until forced apart by pollinator, viscid, mostly glabrous, glandular-lepidote on the ridge at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2 mm long, the longer filaments 1.4–1.6 cm long, the shorter filaments 1.2–1.3 cm long, the staminode 3–4 mm long, inserted 5 mm from the base of corolla tube; pistil 2.1–2.3 cm long, bent near the base, ovary truncate-conical, 2.5 mm long, 2 mm wide, rough-surfaced and lepidote, the ovules multi-seriate in each locule; disc annular-pulvinate, 1.5 mm long, 3.5 mm wide. *Capsule* (*Lehmann 7691*, Cali, Colombia, K) elliptic, compressed, 7.5 cm long and 4 cm wide, the valves woody, densely rugose-tuberculate with the closely packed tubercles ca. 2 mm long, pubescent with dendroid and simple trichomes, appearing yellowish from the trichomes; seed 1.2–1.3 cm long and 4.7–4.9 cm wide, bialate, the wings thin, brown to almost hyaline at the tip, distinct from the darker brown puberulous seed body.

This species is a rarely collected but locally common vine restricted to the tropical wet forest; it ranges from Costa Rica to Argentina. The flowers have been collected in January, July, and August which is no indication of seasonality. This species is closely allied to *A. paniculatum*. The species can be distinguished vegetatively by the conspicuous, persistent pseudostipules, more conspicuous pubescence, and longer trichomes in *A. pannosum*. On Santa Rita Ridge, the two species occur within a kilometer of each other with no indication of introgression.

I have seen only a fragment of the type of *Bignonia pannosa*, but a photograph of the type specimen agrees with the Central American material. Acceptance of the name *A. pannosum* is also based on Sandwith's notation on a herbarium sheet of it at Kew (*Haught 3399*) that he had matched that specimen with the Pavon type collection at Madrid (MA). Some recent workers have argued that *A. pannosum* is synonymous with *A. paniculatum* (including *A. macrophyllum*), but until the type is re-examined Sandwith's interpretation should be accepted.

COLÓN: Santa Rita Ridge, *Dwyer & Gentry 9380* (MO); *Dwyer et al. 9037* (MO).

3. ANEMOPAEGMA

Anemopaegma Mart. *ex* Meisn., Gen. 1: 300; 2: 208. 1840, nom. cons. TYPE: *A. mirandum* (Cham.) DC.

Cupulissa Raf., Fl. Tell. 2: 57. 1837, nom. rej. TYPE: *C. grandifolia* (Jacq.) Raf. = *Anemopaegma grandifolia* (Jacq.) Merill & Sandw.

Platolaria Raf., Sylva Tell. 78. 1838, nom. rej. TYPE: *P. flavescens* Raf. = *Anemopaegma orbiculatum* (Jacq.) DC.

Lianas (in Central America), stems with (4–)8 phloem arms in cross section; branchlets terete without interpetiolar glandular fields; pseudostipules foliaceous or lacking. *Leaves* 2–5-foliolate, often with a simple or trifid terminal tendril. *Inflorescence* an axillary or terminal raceme. *Flowers* with the calyx cupular, truncate, usually with glands near the margin; corolla bright to pale yellow, tubular-campanulate, glabrous or glandular-lepidote outside; anthers glabrous, the thecae straight, divaricate; pollen grains simple, ecolpate or 5-colpate, the exine reticulate; ovary ellipsoid, usually stipitate, lepidote or puberulous, the ovules 2–6-seriate in each locule; disc pulvinate. *Fruit* an elliptic to orbicular capsule, the valves parallel to the septum, usually strongly compressed, smooth; seeds flat, completely surrounded by a broad hyaline-membranaceous wing, or wingless and the seed body larger, brown and corky.

About 30 species; continental tropical America from Brazil and Argentina to Mexico. *Anemopaegma* is taxonomically one of the more difficult genera of Bignoniaceae with many species showing great phenotypic plasticity and many of the local phenotypes designated as species. Whether all the morphologically and geographically distinguishable species currently recognized are valid is questionable, but where to draw specific lines is unclear.

a. Leaves palmately 5-foliolate or 4-foliolate with a tendril or tendril scar; fruit suborbicular ..... 3. *A. orbiculatum*
aa. Leaves 2-foliolate, often with a tendril or tendril scar; fruit elliptic or oblong-elliptic (unknown in *A. santa-ritense*).
  b. Pseudostipules foliaceous; tendril simple; leaflets narrowly elliptic; fruit ellipsoidal, not compressed, the seeds corky, wingless ..... 2. *A. chrysoleucum*
  bb. Pseudostipules inconspicuous or lacking; tendril trifid; leaflets ovate to ovate-elliptic; fruit (where known) oblong, compressed, the seeds with broad hyaline membranaceous wings.
    c. Leaves conspicuously pubescent beneath ..... 4. *A. puberulum*
    cc. Leaves glabrous beneath.
      d. Corolla tube glabrous outside; surface of leaflets shiny, varnished-looking, the margin not involute ..... 1. *A. chrysanthum*
      dd. Corolla tube glandular-lepidote outside; surface of leaflets dull, the margin more or less involute ..... 5. *A. santa-ritense*

1. **Anemopaegma chrysanthum** Dugand, Caldasia 4: 307. 1947. TYPE: Colombia, Cauca, Pacific coast, *Cuatrecasas 14269* (COL, holotype; F, isotype).

Liana to at least 2 cm in diameter, the bark smooth, vertically striate; stem with 4 phloem arms in cross section; branchlets subtetragonal, glabrous, the nodes without interpetiolar glandular fields; pseudostipules minute, acute, paired in each axil. *Leaves* 2-foliolate with a tendril or tendril scar; leaflets ovate to ovate-elliptic, acute or shortly acuminate, basally cuneate to rounded with a brief at-

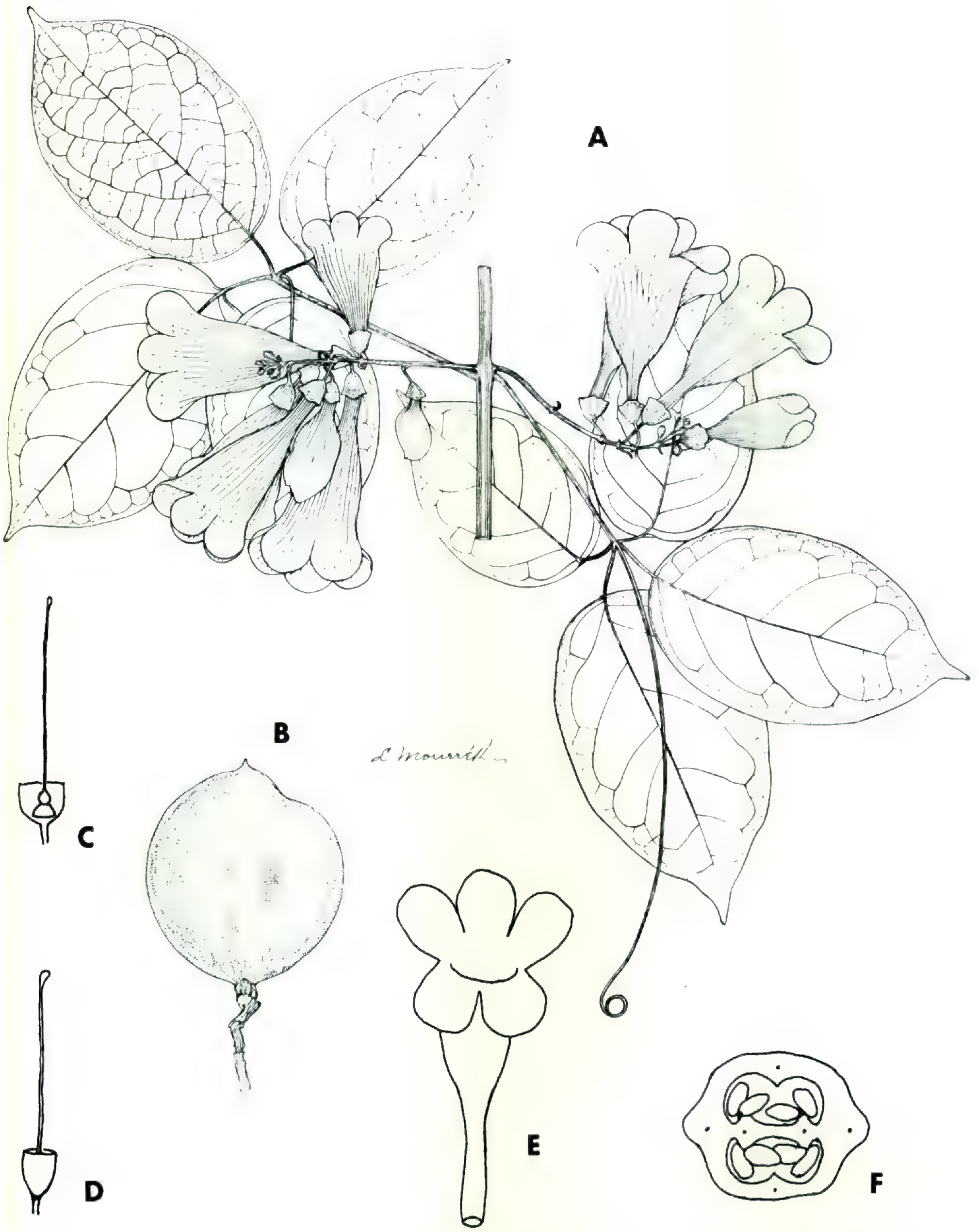

FIGURE 3. *Anemopaegma*.—A–B. *A. orbiculatum* (Jacq.) DC.—A. Habit (× ½). [After *Dressler 4051* (MO).]—B. Fruit (× ⅜). [After *Croat 12742* (MO).]—C–F. *A. chrysoleucum* (H.B.K.) Sandw.—C. Pistil and disc (× ½).—D. Calyx (× ½).—E. Corolla (× ½).—F. Ovary cross section (× 10). [After *Gentry 3848* (MO).]

tenuation at the petiole apex, 9.4–19.5 cm long and 4.7–12.5 cm wide, chartaceous, the secondary veins 4–7 on each side, strongly minute-lepidote beneath, especially in the lower vein axils, usually minutely and inconspicuously scabrous at the base of the main vein above, sometimes beneath, olive when dry, slightly paler be-

neath, above shiny and varnished-looking under a lens; tendril usually trifid, 6–13 cm long to branching, the arms 0.1–1.2 cm long; petiolules ± terete, often twisted, 0.8–3.7 cm long, petiole 2.9–3.9 cm long, somewhat lepidote or minutely subpuberulous. *Inflorescence* a 4–8-flowered, ebracteate axillary raceme; rachis and pedicels somewhat glandular-lepidote, glabrous to minutely subpuberulous at the nodes. *Flowers* with inconspicuous musky odor, calyx cupular, coriaceous, truncate to shallowly 5-lobed, ± lepidote with plate-shaped glands in the upper part, 5–9 mm long and 5–9 mm wide; corolla uniformly bright yellow, tubular-campanulate, 5.2–7.1 cm long and 1.2–2.2 cm wide at mouth of the tube 4.5–5.8 cm long, the lobes 1.1–1.3 cm long, the lobes glandular-lepidote outside and in, the tube glabrous outside, inside sparsely glandular-lepidote near the mouth and pubescent with simple, several-celled, mostly gland-tipped trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4.5 mm long, the longer filaments 2.5–3.2 cm long, shorter filaments 1.9–2.3 cm long, the staminode 6–15 mm long, inserted 11–13 mm from base of corolla tube; pistil 4.2–4.6 cm long, the ovary flattened-cylindric, 6–7 mm long and 2.5 mm wide, 1.5–2.0 mm thick, lepidote, the ovules 2-seriate in each locule; disc annular-pulvinate, 2–2.5 mm long and 6–7 mm wide. *Capsule* oblong-elliptic, flattened, 14–20 cm long and 7.2–8.3 cm wide, the basal stipe 1–2 cm long, drying tan, glabrous; seeds thin, suborbicular, 4–5.5 cm long and 4–5.5 cm wide, the wing not sharply demarcated, membranaceous, marginally hyaline, basally brown, surrounding the seed body.

A plant of the tropical wet forest ranging from southern Mexico to the Pacific coast of Colombia, this species apparently flowers mostly in the dry season. It is rarely collected and has not previously been reported outside Colombia. It can be recognized vegetatively by the large, varnished-looking leaflets, lack of foliaceous pseudostipules, and trifid tendrils.

CANAL ZONE: Pipeline Road, TTC Transect 3, *Gentry 7395* (MO). COCLÉ: N of El Valle de Antón, *Allen 2831* (US). El Valle near La Mesa, *Gentry 7417* (MO). COLÓN: Río Guanche, *Gentry 6315* (MO). Santa Rita Ridge, *Dwyer & Gentry 9374* (MO, SCZ). DARIÉN: Cerro Pirre, *Gentry & Clewell 6964* (MO, PMA). PANAMÁ: Cerro Campana, *Gentry 4907* (MO).

2. **Anemopaegma chrysoleucum** (H.B.K.) Sandw., Lilloa 3: 459. 1938.—FIG. 3C–F.

Bignonia chrysoleuca H.B.K., Nov. Gen. Sp. Pl. 3: 134. 1819. TYPE: Colombia, Río Magdalena, *Humboldt & Bonpland 1576* (P).

Anemopaegma belizeanum Blake, Contr. Gray Herb. 52: 91. 1917. TYPE: British Honduras, Toledo, *Peck 957* (GH).

A. punctulatum Pittier & Standl., Jour. Washington Acad. Sci. 15: 461. 1925. TYPE: Panama, Colón, *Pittier 4009* (GH, NY, US).

A. macrocarpa Standl., Publ. Field Columbian Mus., Bot. Ser. 4: 262. 1929. TYPE: Panama, Bocas del Toro, *Cooper 202* (F, NY, US).

Liana to at least 2.5 cm in diameter, usually less than 1 cm in diameter, the bark smooth, finely longitudinally ridged; stem with 8 phloem arms in cross section; branchlets subterete, longitudinally striate when dry, mostly glabrous, the nodes puberulous, without interpetiolar glandular fields; pseudostipules foliaceous, 4 at each node, 3–13 mm long, 1.5–10.0 mm wide. *Leaves* 2-foliolate

(rarely 3-foliolate), sometimes cirrhose; leaflets narrowly elliptic, acute, cuneate at base, 5.5–15 cm long and 2.0–7.1 cm wide, membranaceous, secondary veins 5–8 on a side, densely lepidote-papillose with scattered, often deciduous, lepidote scales, puberulous on the midvein above, otherwise glabrous, drying olive, concolorous; tendril simple, 8–17 cm long; petiolules 0.3–2 cm long, petiole 0.7–3.4 cm long, puberulous on the upper surface. *Inflorescence* an axillary raceme, often reduced to 3 flowers or a single flower in the leaf axil, the peduncle and pedicels glabrous or inconspicuously lepidote. *Flowers* with a sweet aroma, calyx cupular, truncate, 7–12 mm long and 7–10 mm wide, inconspicuously lepidote to essentially glabrous, inconspicuously ciliate on the margin, usually with submarginal plate-shaped glands, corolla lobes cream-colored, the tube yellow outside, inside yellow with a longitudinal orange stripe below each of the lower 4 sinuses, tubular-campanulate above a narrowed base, 6.2–10.3 cm long and 1.1–2.2 cm wide at the mouth of tube, the tube 4.3–7.5 cm long, the lobes 1.1–2.0 cm long, glabrous outside, inside glandular-lepidote on the lobes, mostly glabrous in the tube, pubescent with simple trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divergent, 3.5–4.5 cm long, the longer filaments 2.3–3.1 cm long, the shorter filaments 1.6–2.1 cm long, the staminode 3–6 mm long; inserted (2.4–)2.7–3.1 mm from base of corolla tube; pistil 5.1–5.6 cm long, the ovary rounded-cylindric, 2.0–2.5 mm long and 2.0–2.5 mm wide, 1.5–2.0 mm thick, densely lepidote, the ovules 4-seriate in each locule; disc conical-pulvinate, 3–4 mm long, 3–4 mm wide at base, 1.5 mm wide at top. *Capsule* elliptic, compressed, acute, 6.2–12.2 cm long and 2.9–6 cm wide, on a stipe 1–1.2 cm long, drying yellow-brown, the surface slightly and inconspicuously lepidote, appearing rough and varnished under a lens, the calyx persistent; seeds 1.4–1.8 cm long and 1.9–2.4 cm wide, woody, somewhat flattened, essentially wingless, the hilum large, elliptic, to 3 mm by 7 mm.

This species is restricted to lowland swampy areas and river banks in the tropical wet forest and wetter parts of the tropical moist forest, ranging from British Honduras to Venezuela. It flowers irregularly throughout the year, most frequently in the wet season, seldom with more than one or two flowers opening at a time. The vine tends to remain slender and can flower when only a few millimeters in diameter and almost herbaceous. The flowers are sweetly aromatic when fresh with an odor resembling that of *Cydista aequinoctialis* but more delicate. The seeds are water-dispersed.

Foliaceous pseudostipules provide the most useful field character. The slender, terete twigs distinguish *A. chrysoleucum* from the angular twigs of other similarly pseudostipulate species of Bignoniaceae.

Anemopaegma chrysoleucum was more broadly interpreted by Sandwith (Kew Bull. 1953: 470. 1954) to include *A. paraense* Bur. & K. Schum. (including *A. surinamense* Sprague *ex* Pulle and *A. grandiflorum* Sprague) of the Guianas and Amazonia. *A. chrysoleucum* has small, membranaceous leaflets, small pseudostipules, and few flowers in an inflorescence. *Anemopaegma paraense* has larger, coriaceous leaflets, larger pseudostipules, and a many-flowered inflorescence. Field study shows that the distinguishing characters of *A. chrysoleucum* are consistent and do not vary from top to bottom of a vine as supposed by Sand-

with. On the other hand, *A. flavum* Morong (= *A. symmetricum* Rusby) of Bolivia and west central Brazil to Argentina is similar to *A. chrysoleucum* and may be conspecific.

BOCAS DEL TORO: Almirante, *Cooper 202* (F, NY, US); *Gentry 2688* (MO). Nances Cay Island, *von Wedel 538* (MO, US). Water Valley, *von Wedel 968* (GH, MO, US). Fish Creek, *von Wedel 2218A, 2356* (both MO), *2445* (GH, MO, US). Shepherd Island, *von Wedel 2674* (GH, MO, US). Western River, *von Wedel 2702* (GH, MO, US). Near Almirante, *Woodson & Schery 1031* (MO). CANAL ZONE: Barro Colorado Island, *Bangham 544* (A); *Croat 12683* (MO); *Shattuck 1131* (MO); *Starry 309* (MO). Near Gatún, *Goldman, 1869* (US). Cãno Quebrado, *Pittier 6669* (US). S of Colón, *Tyson et al. 4490* (MO, SCZ). COLÓN: E of Río Piedras, *Gentry 2188* (MO). Along Río Sirrí, Trinidad Basin, *Pittier 4009* (GH, NY, US). DARIÉN: Near El Real, *Duke 4826, 4915* (both MO), *4936* (MO, SCZ). Between Cerro Pirre and El Real, *Gentry 4784* (MO). Near Marragantí, *Williams 649* (NY, US). PANAMÁ: Río Sulugandí, *Gentry 3745* (MO). Junction of Ríos Espavé and Bayano, *Gentry 3848* (MO). SAN BLAS: Mainland opposite Playón Chico, *Gentry 6382* (MO, PMA).

3. **Anemopaegma orbiculatum** (Jacq.) DC., Prodr. 9: 190. 1845.—FIG. 3A–B.

Bignonia orbiculata Jacq., Sel. Stirp. Amer. Hist. 184, *tab. 180, fig. 79*. 1763. TYPE: Colombia, Cartagena, *Jacquin s.n.* (BM, single leaf which matches illustration).
Jacaranda orbiculata (Jacq.) Spreng., Syst. Veg. 2: 834. 1825.
Platolaria flavescens Raf., Sylva Tell. 78: 1838. TYPE: (not seen).
Pithecoctenium panamense Benth., Bot. Voy. Sulphur 129. 1844. TYPE: Panama, *Sinclair s.n.* (K).
Peltospermum orbiculatum (Jacq.) DC., Prodr. 9: 191. 1845, pro. syn.

Liana to at least 2.5 cm in diameter, the bark light gray, smooth; stem with 8 phloem arms in cross section; branchlets subtetragonal, hollow, longitudinally ridged, puberulous, interpetiolar glandular fields lacking, an interpetiolar ridge sometimes connecting opposite petioles; pseudostipules usually lacking, rarely minutely foliaceous in young branches. *Leaves* digitately 5-foliolate or 4-foliolate with a tendril or tendril scar; leaflets ovate, acuminate, rounded to subcordate, membranaceous to subcoriaceous, secondary veins 5–7(–8) on each side, minutely papillate and impressed-lepidote above and beneath, scabrous along most veins beneath and on the midvein above, drying olive, the terminal leaflet 4.3–22 cm long and 2.2–10 cm wide, intermediate leaflets 4.7–18.2 cm long and 2.3–9.5 cm wide, basal leaflets 3.0–14.5 cm long and 2.1–8.2 cm wide, the terminal petiolule 0.8–5.5 cm long, intermediate petiolules 0.8–3.8 cm long, basal petiolules 0.4–2.6 cm long; petiole 3.2–13.5 cm long, puberulous; tendril simple or trifid, 8–17 cm long, the ends when split, 1–5 mm long. *Inflorescence* a 1–10-flowered axillary or terminal raceme, its branches puberulous. *Flowers* faintly fragrant, calyx cupular, truncate, with 5 irregular, minute, submarginal teeth, 5–8 mm long and 5–9 mm wide, puberulous, sometimes with glands; corolla tube yellow, the lobes cream, without nectar guides, tubular-campanulate, 3.2–5.0 cm long and 1.4–1.9 cm wide at the mouth of tube, the tube 2.6–4.1 cm long, the lobes 0.7–1.0 cm long, strongly glandular-lepidote outside, the trichomes sometimes drying orange, inside scattered glandular-lepidote, pubescent with gland-tipped trichomes at and below the level of stamen insertion; stamens didynamous, the anther thecae more or less divaricate, 3–4 mm long, the longer filaments 2.0–2.6 cm long, the shorter filaments 1.3–1.9 cm long, the staminode 2–7 mm long, inserted 6–11 mm from base of corolla tube; pistil 2.4–3.0 cm long, the ovary stipitate, rounded-cylindric,

2 mm long and 1.5 mm wide, 1 mm thick, lepidote, the ovules 4-seriate; disc conical-pulvinate, 3 mm wide for basal 1 mm, upper 1.5 mm tapering to a 1-mm-wide stipe below ovary. *Capsule* circular with a 1.0–1.5 cm long basal stipe, 7.5–9.5 cm in diameter, flattened, the valves slightly convex, ca. 2 cm thick at the center, the surface smooth, scattered lepidote or lepidote-punctate; seeds circular, 2.8–4.5 cm in diameter with a well demarcated membranaceous wing surrounding the seed body, brownish near the center and hyaline near the margin.

Occurring most commonly in drier parts of the tropical moist forest, this species is also found to some extent in tropical wet forest, mostly in disturbed areas. It ranges from Nicaragua to Colombia, though previously unreported northwest of the Canal Zone. It flowers irregularly throughout the year. The seeds are effectively wind dispersed. This is the only liana of the family in Central America with palmately compound 5-foliolate leaves. The 3-foliolate first seedling leaves are unusual in the Bignonieae.

CANAL ZONE: Pipeline Road, *Correa & Dressler 408* (MO); *Croat 12742* (MO, SCZ); *Gentry 1775* (MO), *1799* (MO, SCZ), *4856* (MO). Ancon Hill, *Duke 4603* (K, MO); *Killip 12110* (US); *Mason s.n.* (US); *Standley 26399* (US); *Williams 37* (NY, US). Near Summit Hills Golf Course, *Gentry 1587, 2820* (both MO). Between Corozal and Ancón, *Pittier 6507* (BM, F, GH, MO, NY, US); *Pittier 6803* (GH, US). Balboa, *Standley 29272* (US). Obispo, *Standley 31774* (US). Near Miraflores, *White 114* (F, GH, MO). DARIÉN: Isla María in Golfo de San Miguel, *Gentry 3999* (MO). Near La Palma, *Gentry 4296* (MO); *Pittier 5493* (NY, US). LOS SANTOS: Loma Prieta, *Duke 11877* (MO); *Lewis et al. 2247* (MO). PANAMÁ: Near Bejuco, *Allen 974* (MO); *Duke 4558* (K, MO). Nueva Gorgona, *Allen 3765* (GH, K, MO, NY). Perlas Islands, without locality, *Anderson 1852* (GH). Between Río Pacora and Chepo, *Dwyer et al. 5092* (MO, NY, SCZ). Perlas Islands, San José Island, *Erlanson 14* (GH, US), *34* (GH, NY, US), *391* (GH, US); *Harlow 40* (GH, US); *Johnston 198* (GH, MO, US), *469* (GH), *668* (GH, US), *714* (GH, MO). Near Río Bayano beyond Cañitas, *Gentry 1664* (MO). Río Piragua (or Tabardí), *Gentry 2550* (MO). Icantí, *Gentry 2619* (MO). Near Río Espavé, *Gentry 3701* (MO). Near Río Partí, *Gentry 3798* (MO). Near Panamá Cruces, *Hayes 132* (BM, K). Near Juan Díaz, *Maxon & Harvey 6736* (BM, US); *Standley 30612* (US). Near Bella Vista, *Piper 5325* (US). Along Corozal road near Panamá, *Standley 26767* (US). WITHOUT LOCALITY: *Cuming 1110* (BM, K); *Hayes 594* (NY); *Seemann s.n.* (K); *Sinclair s.n.* (K).

4. **Anemopaegma puberulum** (Seib.) Miranda, Anal. Inst. Biol. México 24: 93. 1953.

Chodanthus puberulus Seib., Carnegie Inst. Washington Publ. 527: 425. 1940. TYPE: México, Chiapas, Chiapa, *Goldman 999* (US).

Liana, branchlets subterete, puberulous or glabrate, the nodes without interpetiolar glandular fields; pseudostipules small, inconspicuous, paired in each axil. *Leaves* 2-foliolate with a tendril or tendril scar; leaflets ovate-elliptic, acute, the base rounded, 8–13 cm long and 5.6–7.5 cm wide, chartaceous, the secondary veins 3–5 on each side; strongly puberulous beneath, glabrous and shiny above; tendril trifid; petiolules terete, 2.5–3.0 cm long, petiole 2.2–3.1 cm long. *Inflorescence* a several-flowered ebracteate puberulous raceme. *Flowers* with the calyx cupular, subcoriaceous, truncate, puberulous with glands in the upper part, 6–8 mm long and 8–9 mm wide; corolla yellow, tubular-campanulate, 5–5.4 cm long and 1.5–1.6 cm wide at the mouth of tube, the tube 4–4.3 cm long, the lobes 0.8–1.0 cm long, glandular-lepidote inside and out, the tube glabrous except inside

at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, ca. 3 cm long, the longer filaments ca. 2 cm long, the shorter filaments ca. 1.3 cm long, the staminode 3–4 mm long; inserted 8–9 mm from the base of the corolla tube; pistil 3.2–3.3 cm long, ovary narrowly oblong, 3 mm long, 1–1.5 mm wide, lepidote; disc annular-pulvinate, 1 mm long and 2–2.5 mm wide. *Capsule* (Miranda) elliptic-oblong, flattened, puberulent and glandular-lepidote, 12–21 cm long and 6.5–8, cm wide, on a stipe 1.5–2 cm long.

This species was supposedly restricted to Veracruz to Chiapas in southern Mexico and to adjacent Guatemala, although a plant cultivated at Fairchild Tropical Garden, Florida, was reported as acquired from Costa Rica. The single Panamanian collection cited here represents a significant range extension and elimination of most of the disjunction between *A. puberulum* and its South American relative, *A. lehmanii* Sandw. The latter species, known only from the type collection from the Department of Cauca, Colombia, is closely related to and perhaps not distinct from *A. puberulum*, reportedly differing in shorter trichomes, shorter petioles, and larger calyx.

Anemopaegma puberulum apparently differs from *A. chrysanthum* Dugand only in its pubescence, especially on the leaves, and the two may prove to be conspecific.

PANAMÁ: El Llano-Cartí highway, 6–10 km N of El Llano, *Dressler 4329* (MO, PMA)

5. **Anemopaegma santa-ritense** A. Gentry, Ann. Missouri Bot. Gard. 58: 93. 1971. TYPE: Panama, Colón, *Gentry 454* (MO, holotype; WIS, isotype).

Liana, branchlets more or less subtetragonal with the wrinkled surface forming longitudinal ridges when dry, the epidermis finely and regularly papillate with scattered lepidote scales and sometimes a minute puberulence at the nodes, the nodes without interpetiolar glandular fields or pseudostipules. *Leaves* 2-foliolate with a tendril or tendril scar; leaflets ovate, obtuse, short acuminate, basally truncate 5.9–11 cm long and 2.8–5.3 cm wide, coriaceous to chartaceous, the margins revolute, the epidermis regularly and densely papillose with scattered lepidote punctations, the smaller veinlets obscure, glabrous above and beneath to rarely minutely puberulent at the base of the midvein beneath, green to olive above, light green to yellowish beneath, the petiolules 0.6–1.3 cm long, the petiole 1.2–2.5 cm long; tendril usually trifid, rarely simple, 3–12 cm long to branching, the 3 arms 0.4–1.0 cm long. *Inflorescence* an axillary one to few-flowered raceme with opposite flowers. *Flowers* with the calyx cupular, glabrous, truncate, eglandular, 5–8 cm long and 7–9 cm wide; corolla yellow, tubular-campanulate above the narrowed tubular base, 5–7.5 cm long and 1.7–1.9 cm wide at the mouth of tube, the tube 3.8–5.3 cm long, the lobes 0.8–1.1 cm long, lepidote outside, inside lepidote on the lobes, glandular pubescent below the point of stamen insertion and sparsely so on the lobes; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 1.9–2.1 cm long, the shorter filaments 1.7–1.9 cm long, the staminode 0.7–0.9 cm long, inserted ca. 10 mm from base of corolla tube; pistil 4.0–4.2 cm long, the ovary stipitate, flattened-ovate, 2 mm long, 1–1.5

mm wide, 0.5 mm thick; disc conspicuous, conical-pulvinate, 1.5 mm long, 2.5 mm wide. *Capsule* unknown.

This species is known only from the tropical wet forest in central and eastern Panama, mostly above 800 m elevation. Recent sterile collections from Cerro Jefe, Cerro Pirre, and the mountains above Puerto Obaldía are referable to this species, formerly known only from Santa Rita Ridge. Its fruits have never been collected.

Anemopaegma santa-ritense is a puzzling form with close relatives from which it seems to differ consistently, but by only one or two significant characters. Its closest relatives are *A. carrerense* Armitage (possibly = *A. karstenii* Bur. & K. Schum.) and *A. chamberlaynii* (Sims) Bur. & K. Schum., which have leafy pseudostipules and minor leaf differences but are similar in other respects.

COLÓN: Santa Rita Ridge, *Allen 5105* (MO); *Correa & Dressler 772* (MO); *Croat 13832* (MO); *Dressler & Lewis 3721* (MO); *Gentry 454* (MO, WIS), *734*, *735*, *736* (all MO); *Gomez-Pompa et al. 2990*, *3305* (both MO); *Lewis et al. 5288* (MO, SCZ). DARIÉN: Summit of Cerro Pirre, *Gentry 4599* (MO). PANAMÁ: Cerro Jefe, *Gentry 2879* (MO). SAN BLAS: Mountaintop above Puerto Obaldía, *Gentry 1506* (MO).

4. ARRABIDAEA

Arrabidaea DC., Rev. Bign. (Bibl. Univ. Genève) 10. 1838. TYPE: *A. rego* (Vell.) DC.

Chasmia Schott *ex* Spreng., Syst. Cur. Post. 409. 1827, nomen nudum.
Pentelesia Raf., Sylv. Tell. 78. 1838. TYPE: *P. discolor* Raf. = *Arrabidaea carichanensis* (H.B.K.) Bur. & K. Schum.
Vasconcellia Mart., Flora 24(2): Beibl. 12. 1841, nomen nudum.
Cremastus Miers, Proc. Roy. Hort. Soc. 3: 187. 1863. LECTOTYPE: *C. glutinosa* (DC.) Miers = *Arrabidaea sceptrum* (Cham.) Sandw.
Panterpa Miers, Proc. Roy. Hort. Soc. 3: 196. 1863. TYPE: *P. leucopogon* (Cham.) Miers = *Arrabidaea leucopogon* (Cham.) Sandw.
Petastoma Miers, Proc. Roy. Hort. Soc. 3: 194. 1863. TYPE: *P. samydoides* (Cham.) Miers = *Arrabidaea samydoides* (Cham.) Sandw.
Paramansoa Baill., Hist. Pl. 10: 27. 1888. TYPE: *P. grosourdyana* Baill. = *Arrabidaea grosourdyana* (Baill.) Sandw.

Lianas, rarely shrubs or small trees, stems with 4 phloem arms in cross section; branchlets terete, usually with interpetiolar glandular fields; pseudostipules small and inconspicuous. *Leaves* usually 3-foliolate, the terminal leaflet often replaced by a simple tendril. *Inflorescence* usually a large, many-flowered axillary or terminal panicle. *Flowers* with the calyx cupular, truncate, usually minutely 5-denticulate, pubescent; corolla pale pink to purple (white-flowered forms in some species), relatively small, more or less campanulate, densely pubescent outside at least on the lobes; anthers glabrous, the thecae straight or slightly curved, usually divaricate; pollen grains single, tricolpate, the exine finely granular or punctate; ovary narrowly cylindrical, usually minutely lepidote, the ovules 2-seriate; disc cupular-pulvinate. *Fruit* a compressed, linear capsule, the valves parallel to the septum, essentially smooth, usually with a slightly raised median nerve; seeds bialate, the wings usually more or less hyaline and distinct from the seed body.

About 70 species ranging in tropical America from Mexico and the West Indies (rare) to Argentina.

a. Capsule valves without noticeably raised median nerve, softly puberulous or with sharply angled margins; corolla usually over 3.5 cm long, the tube pubescent outside; calyx usually drying dark with lighter or thinner rim.
b. Capsule valves pubescent, the margins not angled; calyx evenly 5-denticulate with a white-fringed margin ..... 6. *A. mollissima*
bb. Capsule valves glandular-pitted, the margins sharply angled; calyx unevenly truncate to sub-bilabiate, not evenly denticulate, thinner at the margin but not evenly whitish-fringed ..... 4. *A. corallina*
aa. Capsule valves with somewhat raised median nerve, glabrous or lepidote, the margins rounded; corolla usually less than 4 cm long (if longer, the tube glabrous); calyx rim not noticeably lighter or thinner than rest of calyx when dried.
c. Corolla tube glabrous outside, dark in bud with a conspicuous white tip from the pubescence of the lobes; calyx reflexed away from base of corolla; leaves simple or 2-foliolate ..... 8. *A. patellifera*
cc. Corolla tube pubescent outside, the buds not bi-colored; calyx cupular, enclosing base of corolla; leaves always 3-foliolate in part, never simple.
d. Leaflet underside conspicuously whitish from the dense short puberulence, the main veins less puberulous and drying brownish or tan and conspicuously darker than the lamina ..... 1. *A. candicans*
dd. Leaflets variously pubescent or glabrate but undersides not conspicuously whitish in contrast with the darker main veins.
e. Leaflets (including veins) evenly and densely tannish-puberulous beneath; corolla less than 1.8 cm long; capsule usually less than 9 cm long ..... 9. *A. pubescens*
ee. Leaflets glabrate or pubescent mostly along the main nerves beneath (if in part tannish-puberulous, then the corolla more than 2.2 cm long); mature capsules usually more than 9 cm long.
f. Leaves drying conspicuously brick red at least in patches, usually glabrous except for simple trichomes in axils of lateral nerves beneath; interpetiolar glandular fields present ..... 2. *A. chica*
ff. Leaves not drying reddish, usually slightly puberulous at least along main veins below; interpetiolar glandular fields present or absent.
g. Mature branchlets with loose, conspicuously wrinkled epidermis and inconspicuous lenticels, young branchlets drying black with contrasting light lenticels; inflorescence contracted, few-flowered (3–7(–25)-flowered including buds) ..... 7. *A. oxycarpa*
gg. Mature branchlets with tight, finely, and evenly striate epidermis with noticeable small lenticels; young branchlets drying grayish or brownish; inflorescence open, many-flowered.
h. Corolla less than 2 cm long; calyx drying grayish, eglandular, small (3–4 mm long and 2–3 mm wide); inflorescence branches long-pedunculate (1–5 cm), the peduncles terminated by dense ultimately trichotomous corymbs; capsule drying blackish, 0.8–1.0 cm wide; seed wings hyaline-membranaceous; usually without interpetiolar glandular fields ..... 5. *A. florida*
hh. Corolla more than 2.2 cm long; calyx drying whitish-gray with conspicuous submarginal darker glands, larger (4–7 mm long and 4–6 mm wide); lateral branches of inflorescence narrow, subracemose, without elongate peduncles, the flowers borne along their length; capsule drying brownish, more than 1.0 cm wide at maturity; seed wings basally brownish with hyaline tips; usually with interpetiolar glandular fields ..... 3. *A. conjugata*

1. **Arrabidaea candicans** (L. C. Rich.) DC., Prodr. 9: 185. 1845.—FIG. 4D–H.

Bignonia candicans L. C. Rich., Act. Soc. Hist. Nat. Paris 1: 110. 1792. TYPE: French Guiana, *LeBlond s.n.* (P).

B. colorata Poir. *in* Lam., Encycl. Bot. Suppl. 1: 634. 1800. TYPE: French Guiana, ex herb. Poiret (P).

Arrabidaea candicans var. *latifolia* DC., Prodr. 9: 186. 1845. TYPE: French Guiana, *Perrottet s.n.* (BM, P).

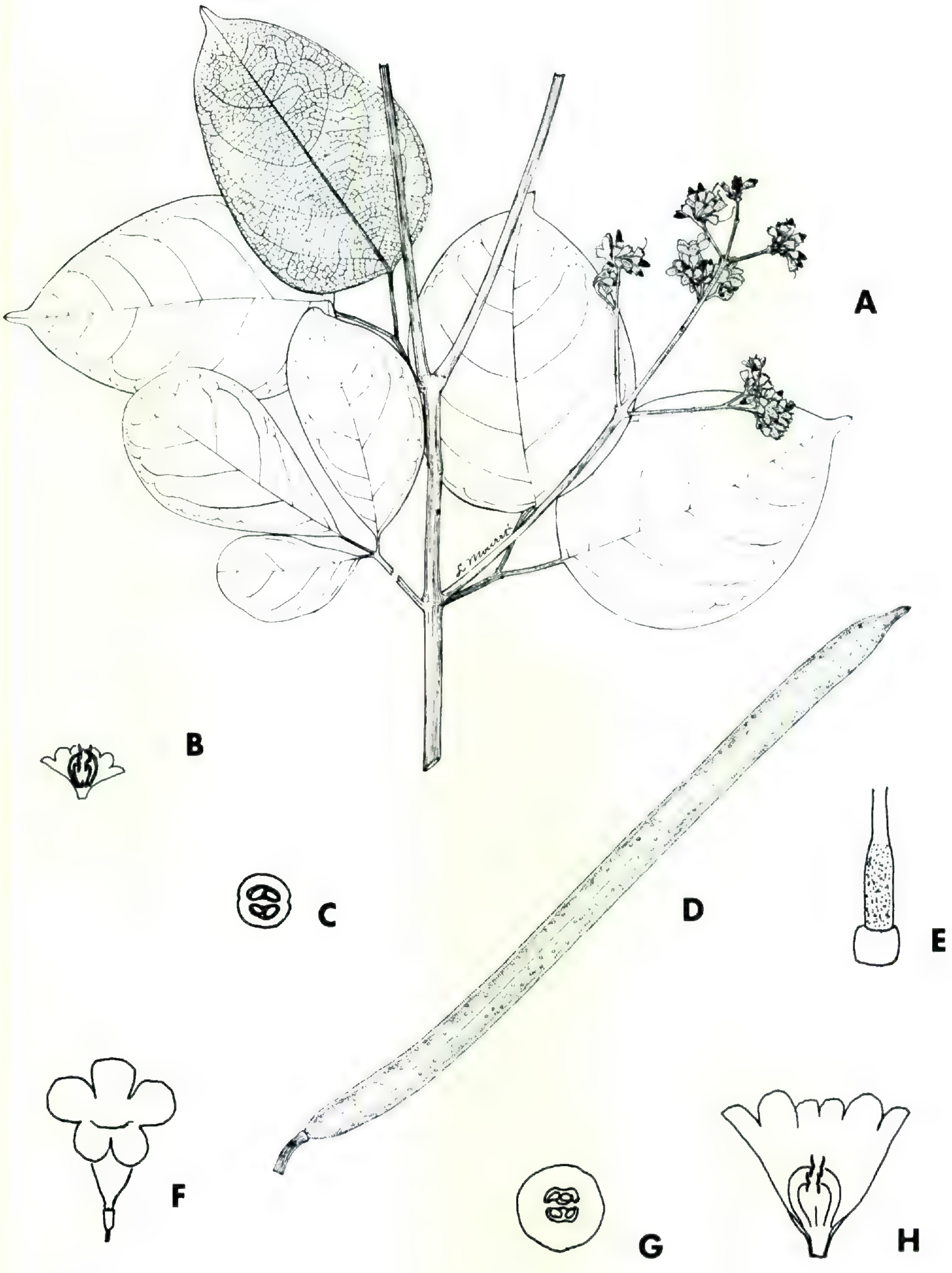

FIGURE 4. *Arrabidaea*.—A–C. *A. florida* DC.—A. Habit ($\times$ 3/5).—B. Corolla split open ($\times$ 3/5).—C. Ovary cross section ($\times$ 12). [After *Gentry 3120* (MO).]—D–H. *A. candicans* (L. Rich.) DC.—D. Fruit ($\times$ 1/2). [After *Croat 5228* (MO).]—E. Ovary and disc ($\times$ 6).—F. Flower ($\times$ 3/5).—G. Ovary cross section ($\times$ 12).—H. Corolla split open ($\times$ 3/5). [After *Gentry 2865* (MO).]

A. orbignyana DC., Prodr. 9: 184. 1845. TYPE: Bolivia, Santa Cruz, *d'Orbigny 1135* (P).
A. subincana DC. sec. Seem., Bot. Voy. Herald 180. 1854, non DC.
A. pruinosa Kl. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 57. 1896. TYPE: British Guiana, *Schomburgk 433* (not seen).
A. schomburgkii Kl. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 58. 1896. TYPE: British Guiana, *Schomburgk 1332* (K).
A. pachycalyx Sprague, Bull. Herb. Boiss., sér. 2. 6: 373. 1906. LECTOTYPE: Colombia, Magdalena, *H. H. Smith 744* (BM, BR, GH, K, MO, NY, P, US).
A. rhodothyrsus Kränzl., Fedde Repert. 17: 20. 1921. TYPE: Costa Rica, Guanacaste, *Tonduz 13643* (BM, F, GH, K, NY, US).
A. calodictyos Sprague, Kew Bull. 1927: 358. 1927. TYPE: Venezuela, Distrito Federal, *Pittier 11883* (K).
A. zulianensis Pittier, Jour. Washington Acad. Sci. 18: 341. 1928. TYPE: Venezuela, Zulia, *Pittier 10992* (US, VEN).

Liana to 7 cm in diameter, the bark yellowish to pale gray, smooth, 4-furrowed in age; stem with 4 phloem arms in cross section; branchlets subterete with raised warty lenticels, minutely puberulous when young, soon glabrate, interpetiolar glandular fields conspicuous; pseudostipules lacking. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ± ovate, membranaceous to chartaceous, secondary veins (4–)5–6(–9) on a side, above glabrate, minutely puberulous at the base of the midvein, drying grayish-brown to reddish-brown, beneath densely white puberulous, less so on the main veins, the short simple trichomes completely covering the surface, drying whitish from the pubescence with contrasting darker main veins, the terminal leaflet acuminate to subretuse, broadly cuneate to truncate, 6.2–15.5 cm long and 4.2–9.1 cm wide; the lateral leaflets acute to retuse, broadly cuneate to asymmetrically subcordate, 5.8–14.8 cm long and 3.6–10.7 cm wide; the terminal petiolule 1.0–3.3 cm long, the lateral petiolules 0.8–3.2 cm long, the petiole 1.6–6.1 cm long, minutely puberulous as the petiolules; tendril simple, 11–21 cm long. *Inflorescence* a terminal or axillary panicle, its branches puberulous. *Flowers* with a sweet aroma, calyx cupular, simple puberulous and lepidote, mostly with some glands, truncate to minutely subdenticulate, 3–6 mm long and 2–4 mm wide; corolla magenta with white throat, tubular-campanulate, 2.2–4.0 cm long and 0.8–1.4 cm wide at the mouth of tube, the tube 1.4–2.7 cm long, the lobes 0.4–1.0 cm long, moniliform pubescent outside and on lobes inside, the tube mostly glabrous, sparsely pubescent in the floor of throat with several-celled simple or rarely forked trichomes, and at the level of stamen insertion with long simple gland-tipped trichomes; stamens didynamous, inserted 5–6 mm from base of corolla tube, the anther thecae divaricate, 2–2.5 mm long, the longer filaments 1.5–1.6 cm long, the shorter filaments 1.1–1.4 cm long, the staminode 4–6 mm long; pistil 1.7–1.8 cm long, the ovary linear oblong, 2–2.5 mm long and 0.5–1.0 mm wide, finely lepidote, the ovules 2-seriate; disc cupular-pulvinate, ca. 1 mm long and 1 mm wide. *Capsule* linear, acuminate, flattened, 12–35 cm long and 0.8–1.3 cm wide, the surface slightly warty and with lepidote glands, the midrib and margins slightly raised; seeds 0.6–1.0 cm long and 2.0–3.4 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A common liana typical of the tropical moist forest, *A. candicans* occurs also sporadically in the tropical wet forest and pre-montane wet and moist forest. It ranges from southern Mexico to Brazil. This species flowers during the early dry

season from November through February. The fruits mature and seeds are released in the late dry season.

The whitish pubescence of the leaf undersurface of this species is its best recognition mark. When dry the main veins are darker than the more pubescent ground surface in contrast to *A. pubescens*, which has veins and undersurface equally pubescent, with a more tannish color. On young leaves of *A. candicans* whitish pubescence may not be obvious except under a lens.

Arrabidaea calodictyos is apparently a partially glabrescent form of this species. It is intermediate between *A. candicans* and *A. chica* and could be a result of hybridization between the two species. Sandwith identified many of these intermediates with *A. chica* rather than *A. candicans*.

CANAL ZONE: Barro Colorado Island, *Brown 123, 128* (both F); *Croat 4833* (SCZ), *5228* (MO, SCZ), *7201* (MO, NY, SCZ), *7329* (MO), *7347, 7698A* (both MO, SCZ), *7884* (MO), *7902, 8124* (both MO, SCZ), *8312* (MO, NY, SCZ), *8375* (MO), *11099* (MO, SCZ), *12592, 12631* (both MO), *12705* (MO, NY); *Dwyer et al. 8441, 8457* (both MO); *Foster 681, 1416* (both PMA); *Gentry 435* (MO, WIS); *Graham 200* (GH); *Oppenheimer & Hladik 97* (MO); *Shattuck 499* (F, MO, US); *Standley 41071* (US); *Wetmore & Abbe 2* (F), *13* (A, F, MO), *27* (F), *58* (A, MO); *Wetmore & Woodworth* 27, *848* (both A). Along road to Venado Beach, *Gentry 2865* (MO). Road to Gamboa airfield, *Gentry 3267* (MO). Río Grande Station, Panamá Railroad, *Hayes s.n.* (BM). Near the Mindí, *Hayes 589* (NY). Howard Air Force Base, *Nowicke et al. 3608A* (MO, SCZ). Along Las Cruces Trail between Fort Clayton and Corozal, *Standley 29226* (US). CHIRIQUÍ: Near San Félix, *Pittier 5129* (NY, US). COCLÉ: 2 miles E of Río Hondo, *Gentry 2907* (MO). Between Aguadulce and Chico River, *Pittier 5003* (NY, US). 1–5 miles S of Antón, *Tyson & Blum 2575, 2776* (both MO, SCZ). COLÓN: 1.5 miles E of Río Piedras on road to Portobelo, *Gentry 2191* (MO). Río Agua Sucio, *Gentry 3195* (MO). Between Río Piedras and Puerto Pilón, *Lewis et al. 3220* (MO, SCZ). DARIÉN: Isla Encanto in Golfo de San Miguel, *Gentry 4013* (MO). S of Jaqué, *Gentry 4120, 4127* (both MO). Río Jaqué 1–2 hours upriver from Jaqué, *Gentry 4186* (MO). Upriver from Boca de Cupe on Río Tuira, *Gentry 4321* (MO). El Real, *Gentry 4565* (MO). HERRERA. Vicinity of Ocú, *Allen 4070* (K, MO). Road from La Arena to outskirts of Pesé, *Burch et al. 1284* (GH, US). S of Ocú, *Gentry 3125* (MO). E of Las Minas, *Gentry 3127* (MO). PANAMÁ: Vicinity of Pacora, *Allen 1113* (GH, MO, NY, US). Río Las Lajas, *Allen 2038* (F, GH, MO, NY, US). Along road between Panamá and Chepo, *Dodge et al. 16625* (BR, K, MO, U). Trail S from Pacora along Río Pacora, *Gentry 1410, 1411* (both MO). Río Pasiga, *Gentry 2199, 2247, 2260* (all MO). Río Maestro, *Gentry 2235* (MO). Río Piragua (Tabardí), *Gentry 2576* (MO). 10–15 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3821* (MO). W of Chepo, *Gentry & Tyson 1640* (MO). Dam site on Río Bayano, *Gentry & Tyson 1663B* (MO). San José Island, *Johnston 969* (BM, GH, MO, US), *1324, 1407* (both GH, MO, US). San Francisco de la Caleta, *Paul 237* (US). Near Panamá, *Sargent s.n.* (US). Near Punta Paitilla, *Standley 26310* (MO, US). E of Río Tocumen, *Standley 26691* (BM, GH, US). Tumba Muerto Road near Panamá, *Standley 29729* (GH, US). VERAGUAS: Hills W of Soná, *Allen 1029* (GH, MO, NY, US). 25 mi. W of Aguadulce, *Gentry 2922* (MO). Near Santiago, *Seemann 152* (K). WITHOUT LOCALITY: *Duchassaing s.n.* (K, P), *Seemann 152* (K).

2. **Arrabidaea chica** (H. & B.) Verl., Rev. Hortic. 40: 154. 1868.

Bignonia chica H. & B., Pl. Aequin. 1: 107, *pl. 31*. 1808. TYPE: Venezuela, Orinoco, *Humboldt & Bonpland s.n.* (P).
B. cuprea Cham., Linnaea 7: 655. 1832. TYPE: Brazil, *Sellow s.n.* (K).
Arrabidaea acutifolia DC., Prodr. 9: 185. 1845. TYPE: Brazil, São Paulo, *Martius s.n.* (M).
A. rosea DC., Prodr. 9: 185. 1845. SYNTYPES: Brazil, São Paulo, *Guillemin s.n.* (not seen); Amazonas, *Martius s.n.* (M).
Bignonia triphylla Willd. sec. DC., Prodr. 9: 151. 1845, pro syn, non L. nec Vell.
Temnocydia carajura Mart. *ex* DC., Prodr. 9: 185. 1845, pro syn.
Vasconcellia acutifolia Mart. *ex* DC., Prodr. 9: 185. 1845, pro syn.
Lundia chica (H. & B.) Seem., Bot. Voy. Herald 180. 1854.

Adenocalymma portoricensis Stahl, Est. 6: 186. 1888. TYPE: Puerto Rico (not seen, fide Britton, Sci. Surv. Puerto Rico & Virgin Islands 6. 1925).
Bignonia erubescens S. Moore, Trans. Linn. Soc., ser. 2. 4: 412. 1895, non DC.
Arrabidaea larensis Pittier, Jour. Washington Acad. Sci. 18: 336. 1928. TYPE: Venezuela, Lara, *Jahn 1186* (GH, US, VEN).
A. cuprea (Cham.) Born., Revista Sudamer. Bot. 2: 10. 1935, non Pittier.

Liana to 6 cm in diameter, the bark pale gray, smooth, 4-furrowed in age; stem with 4 phloem arms in cross section, the pith reddish, even when fresh; twigs subterete with raised warty lenticels, glabrous to subpuberulous, the younger branchlets drying reddish black, interpetiolar glands usually present but often inconspicuous except on very young twigs; pseudostipules not noticeable. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate to narrowly ovate, acuminate to acute, cuneate to truncate, membranaceous, secondary veins 5–7 on a side, above glabrous, sometimes minutely scabrous at the base of midvein, glabrous beneath except for simple trichomes in the axils of lateral nerves or sometimes slightly scabrous along main veins, rarely puberulous on the surface, dark glossy green when fresh, green with red mottling to uniformly brick red when dry; the terminal leaflet 4.4–12 cm long and 1.3–7.0 cm wide; lateral leaflets 3.3–11.5 cm long and 1.3–5.5 cm wide, petiole and petiolules glabrous to subpuberulous, the terminal petiolule 0.6–4.6 cm long, the laterals 0.3–2.1 cm long, the petiole 1.5–7.1 cm long; tendril simple, 6–12 cm long. *Inflorescence* a terminal panicle, its branches puberulous. *Flowers* aromatic, calyx simple-puberulous, mostly eglandular, truncate to minutely subdenticulate, 3–5 mm long and 2–3 mm wide; corolla 1.6–3 cm long and 0.5–1.4 cm wide at the mouth of tube, the tube 1.1–2.1 cm long, the lobes 0.6–1.2 cm long, pubescent, the tube pubescent outside, mostly glabrous inside, pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 1.5–2 mm long, the longer filaments 1.1–1.3 cm long, shorter filaments 0.9–1.0 cm long, the staminode 3–4 mm long, inserted 3–4 mm from base of corolla tube; pistil 1.1–1.3 cm long, the ovary narrowly cylindric, finely lepidote, 2–2.5 mm long and 0.5–1.0 mm wide, the ovules 2-seriate; disc cupular, 1 mm long, 1 mm wide. *Capsule* linear, acute, flattened, 12–23 cm long and 0.9–1.2 cm wide, the surface smooth, slightly irregular-ridged longitudinally, midrib and margins slightly raised, drying brown to reddish brown, lepidote; seeds thin, bialate, 0.7–0.9 cm long and 2.3–2.6 cm wide, the wings hyaline-membranaceous, distinct from the often reddish-drying body.

This vine is most abundant in tropical wet forest and premontane wet forest but also occurs sporadically in wetter parts of the tropical moist forest. It ranges from Mexico to Brazil and Argentina. It flowers at the end of the dry season and through most of the wet season from mid-April to October.

The leaves of the plant are widely used among tropical Indians as a cosmetic to color the skin red. A note on *Duke 14406* reports additional Cuna uses to include protection against sunburn and a medication used between the toes against "mazamora."

The bright red color (sometimes only in patches) of the dry leaves is an obvious herbarium distinguishing character. When fresh, the plant is relatively difficult to recognize but the combination of mostly 3-foliolate leaves, narrow dark green leaflets, and interpetiolar glandular fields makes recognition possible.

This is another of the species of Bignoniaceae with taxonomically confusing pubescence forms. The leaves range from essentially glabrous to bearded in the axils beneath (commonest) to puberulous over the lower leaf surface. The latter form intergrades with *A. candicans*.

BOCAS DEL TORO: Water Valley, *von Wedel 160* (GH, MO), *899* (GH, MO, US). Shepherd Island, *von Wedel 2676A, 2697* (both GH, MO, US). CANAL ZONE: Barro Colorado Island, *Croat 5038, 6258* (both MO, NY, SCZ), *9266* (MO), *11791* (MO, SCZ); *Foster 931* (PMA). CHIRIQUÍ: Remedios, *Seemann 1610* (GH). COCLÉ: Distrito de la Pintada, *Escobar s.n.* (MO, PMA). DARIÉN: Outskirts of La Palma, *Gentry 3932* (MO). S of Jaqué, *Gentry 4138* (MO). Summit of Cerro Pirre, *Gentry 4675* (MO). Manené to the mouth of Río Cuasi, *Kirkbride & Bristan 1471* (MO). PANAMÁ: La Victoria hills E of Panama City, *Allen 4454* (GH, MO, P). Piriá, *Duke 14406* (SCZ). Near Río Espavé, *Gentry 3716* (MO). Between Ríos Espavé and Sulugandí, *Gentry 4987* (MO). San José Island, *Harlow 28* (GH, US); *Johnston 14* (BM, GH, MO, US). SAN BLAS: Near stream above Puerto Obaldía, *Gentry 1535* (MO). VERAGUAS: Mountains N of Santa Fé, *Gentry 2995, 3086A* (both MO).

3. **Arrabidaea conjugata** (Vell.) Mart., Flora 24(2): Beibl. 46. 1841.

Bignonia conjugata Vell., Fl. Flum. 245. 1825; 6: *Tab. 18.* 1827. TYPE: Brazil (not seen).
B. farinosa Salzm. *ex* DC., Prodr. 9: 185. 1845, pro syn.
Arrabidaea virescens DC., Prodr. 9: 1184. 1845. TYPE: Brazil, Bahia, *Blanchet s.n.* (G-DC).
A. virescens var. *farinosa* DC., Prodr. 9: 185. 1845. TYPE: Brazil, Bahia, *Salzmann 395* (G-DC).
Adenocalymma paniculatum Benth. *ex* Miers, Ann. Mag. Nat. Hist., ser. 3. 7: 393. 1861. TYPE: Brazil, Para, *Spruce s.n.* (NY, W).
Bignonia ciliata Wawra, Oester. Bot. Zeitschr. 12: 237. 1862. TYPE: Brazil (not seen, fide Bureau & K. Schumann, 1896–97).
Arrabidaea amazonica K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 213. 1894, nomen subnudum. TYPE: Brazil (not seen, fide Bureau & K. Schumann, 1896–97).
A. chironeura Bur., Bull. Soc. Bot. France 58, Mém. 3f: 517. 1911. TYPE: Brazil, Rio de Janeiro, *Glaziou 4707* (P).

Liana; stem with 4 phloem arms in cross section; branchlets terete, puberulous or glabrate, usually with conspicuous interpetiolar glandular fields, these sometimes reduced or almost lacking; pseudostipules short, obtuse, not conspicuous. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets elliptic or ovate-elliptic, acute to acuminate, basally rounded, 9–21 cm long and 4.5–12.2 cm wide, membranaceous to chartaceous, secondary veins 4–6 on a side, underside ± glabrous to densely puberulous, the main veins puberulous, above glabrous or with a few short trichomes above the main veins, scattered lepidote on both sides with some plate-shaped glands scattered along midvein beneath, drying dark olive above and green or greenish olive beneath; petiolules 0.7–4.2 cm long, petiole 3–13 cm long, puberulous to glabrate. *Inflorescence* a terminal panicle of numerous narrow subsidiary panicles, the branches puberulous. *Flowers* fragrant, calyx cupular, truncate, minutely 5-denticulate, 4–7 mm long and 4–6 mm wide, drying whitish gray, puberulous outside, usually with a subapical row of dark drying glands; corolla magenta, white inside the tube, tubular-campanulate, 2.2–4.0 cm long and 0.6–1.1 cm wide at the mouth, the tube 1.6–2.9 cm long, pubescent outside mostly glabrous inside, somewhat pubescent at the point of stamen insertion, the lobes 3–8 mm long, pubescent; stamens didynamous, the anther thecae straight, slender, divaricate, 2–2.5 mm long, the longer filaments 1.5–1.7 cm long, the shorter filaments 1.0–1.2 cm long, the staminode 6–7 mm long, inserted 5–6 mm from the base of the corolla tube; pistil 1.7–1.8 cm long, the ovary cylindrical,

lepidote, 2 mm long and 1 mm wide, the ovules 2-seriate in each locule; disc cupular-pulvinate, 0.5–1 mm long and 1.5–2 mm wide. *Capsule* linear, compressed, acuminate, the median nerve and margins slightly raised, 12–31 cm long and 1.1–1.4 cm wide; seeds thin, bialate, 0.7–1.1 cm long and 1.9–2.7 cm wide, the wings brown except for a terminal hyaline-membranaceous fringe.

A liana of sporadic occurrence in the tropical moist forest and gallery forests of the premontane moist and tropical dry forest, it ranges from Costa Rica to Brazil. This species flowers in the wet season from July to September. The seeds are released in the dry season.

Like most species of *Arrabidaea*, *A. conjugata* is difficult to distinguish vegetatively. The dark green, ovate, glabrate leaves provide the best character, but it can be differentiated in the field only with experience. The inflorescence with its narrow lateral branches and whitish calyces, usually with dark submarginal glands, is quite distinctive.

I have seen no type material and have accepted the interpretation of Martius (ex herb.) as to the application of this Vellozo name. The application of this name to this species has also been accepted by many other authors. Should the name *Bignonia conjugata* prove referable elsewhere, *Arrabidaea virescens* DC. would be the correct name for this species.

CANAL ZONE: Near Juan Mina, Flat Rock, Chagres River, *Bartlett & Lasser 16837* (MO). Mohinga Swamp, *Bartlett & Lasser 16825* (MO). West arm of Quebrada Salamanca, *Dodge et al. 17004* (BM, BR, MO, U). DARIÉN: Río Sabana above Santa Fé, *Duke 14093* (MO). Santa Fé, *Gentry 4077* (MO). PANAMÁ: Río Bayana, altos de Maje, Isla Gorgas, *Galindo B-2* (MO).

4. **Arrabidaea corallina** (Jacq.) Sandw., Kew Bull. 1953: 460. 1954.

Bignonia dichotoma Jacq., Enum. Pl. Carib. 25. 1760; Select. Stirp. Amer. Hist. 183. 1763, non *Arrabidaea dichotoma* (Vell.) Bur. TYPE: (not seen, possibly represented by one of the 2 sheets of *B. corallina* at W).

B. corallina Jacq., Fragm. Bot. 37, *tab. 42, fig. 1.* 1800–1809. TYPE: Venezuela, Caracas, *Jacquin s.n.* (W).

B. glabrata H.B.K., Nov. Gen. Sp. Pl. 3: 137. 1819. TYPE: Venezuela, Cumaná, *Humboldt & Bonpland 53* (P).

B. obliqua H.B.K., Nov. Gen. Sp. Pl. 3: 135. 1819. TYPE: Venezuela, Laguna de Valencia, *Humboldt & Bonpland 782* (P).

B. villosa Vahl sec. Spreng., Syst. Veg. 2: 830. 1825, non Vahl.

B. hibiscifolia Cham., Linnaea 7: 705. 1832. TYPE: Brazil, *Sellow s.n.* (not seen, fide Sandw.).

Arrabidaea obovata DC., Prodr. 9: 185. 1845. TYPE: Brazil, Bahia, *Martius s.n.* (M).

Bignonia balbisiana DC., Prodr. 9: 153. 1845. TYPE: Colombia, Magdalena, *Bertero s.n.* (G-DC, MO).

B. rotundata DC., Prodr. 9: 163. 1845. TYPE: Brazil, Bahia, *Blanchet 2757* (K, MO, NY, P).

Cremastus balbisianus (DC.) Miers, Proc. Roy. Hort. Soc. 3: 187. 1863.

Arrabidaea obliqua (H.B.K.) Bur., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 99. 1893.

Bignonia colombiana Morong *in* Morong & Britton, Ann. New York Acad. Sci. 7: 186. 1893. TYPE: Paraguay, Pilcomayo River, *Morong 1535* (MO, NY).

Arrabidaea rotundata (DC.) Bur. *ex* Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 213. 1894.

Cuspidaria hibiscifolia (Cham.) Bur. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894.

Tabebuia chapadensis S. Moore, Trans. Linn. Soc., ser. 2. 4: 422. 1895. TYPE: Brazil, *Moore 79* (BM).

Arrabidaea rhodantha Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 44. 1896. SYNTYPES: Paraguay, along Río Paraguay, *Balansa 499* (K); near Concepción, *Kuntze s.n.* (not seen); Brazil, Matto Grosso, *Kuntze s.n.* (not seen).
A. praecox Hassl., Bull. Herb. Boiss., sér. 2. 6 (append. 1): 25. 1898. TYPE: Paraguay, *Hassler 840* (K).
Bignonia boliviana Rusby, Bull. Torrey Bot. Club 27: 70. 1900. TYPE: Bolivia, junction of Beni and Madre de Dios Rivers, *Rusby 1142* (GH, K, NY, US).
B. acuminata Johnston, Proc. Amer. Acad. Arts 40: 696. 1905. TYPE: Venezuela, Margarita Island, *Johnston 345* (F, GH, K, M, NY, US).
Arrabidaea acuminata (Johnston) Urb., Fedde Repert. 14: 306. 1916.
Adenocalymma friesiana Kränzl., Fedde Rep. 17: 115. 1921. SYNTYPES: Argentina, *Fries 446B* (S, fide Fabris, Rev. Mus. La Plata 9: 383. 1965); *Lorentz & Hieronimus 435* (CORD, fide Fabris Rev. Mus. LaPlata 9: 383. 1965.).
Arrabidaea barquisimetensis Pittier, Jour. Washington Acad. Sci. 18: 339. 1928. TYPE: Venezuela, Lara, *Saer d'Héguert 214* (K, VEN).
A. guaricensis Pittier, Jour. Washington Acad. Sci. 18: 337. 1928, pro parte. TYPE: Venezuela, Guarico, *Pittier 11308* (leaves only) (GH, US, VEN).
A. lenticellosa Pittier, Jour. Washington Acad. Sci. 18: 340. 1928, non Bur. & K. Schum. SYNTYPES: Venezuela, Guarico, *Pittier 12481* (GH, K, US, VEN), *12370* (GH, VEN).
A. ovalifolia Pittier, Jour. Washington Acad. Sci. 18: 337. 1928. TYPE: Venezuela, Aragua, *Pittier 12311* (G, GH, K, US, VEN).
A. spraguei Pittier, Jour. Washington Acad. Sci. 18: 339. 1928. TYPE: Venezuela, Aragua, *Pittier 11476* (K, US, VEN).
Piriadacus hibiscifolius (Cham.) Pichón, Bull. Soc. Bot. France 92: 226. 1945.
Arrabidaea obliqua var. *hirsuta* (DC.) Dugand, Mutisia 9: 3. 1952.
A. rhodantha var. *oxyphylla* Sprague *ex* Sandw., Kew Bull. 1953: 460. 1954, pro syn.

Liana to 7 cm in diameter, the bark gray, rather smooth; stem with 4 phloem arms in cross section; branchlets terete with raised lenticels, glabrous or glabrate, nodes with or without interpetiolar glandular fields; pseudostipules short and inconspicuous. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar, sometimes simple on young plants; leaflets ovate, acute to obtuse, truncate to subcordate or broadly cuneate at base, 3.1–18.2 cm long and 2.3–11.6 cm wide, membranaceous to subcoriaceous, secondary nerves 4–7 on a side, variably pubescent, from glabrate to strongly tannish-pubescent, especially in nerve axils beneath, drying olive to gray, the pubescent form olive to tannish; tendril simple, 8–15 cm long; petiolules 0.6–4.0 cm long, petiole 2.3–3.6 cm long, puberulous. *Inflorescence* a series of narrow axillary panicles in the axils of fallen leaves, the branches puberulous; buds minutely 5-parted with an acuminate tip. *Flowers* with the calyx cupular, bilabiately subtruncate or with 5 inconspicuous teeth, 5–8 mm long and 5–8 mm wide, minutely lepidote and somewhat scabrous, the lobes often with tufts of pubescence; corolla lavender to magenta, the tube white within, tubular campanulate, 2.7–4.6 cm long and 0.8–1.2 cm wide at the mouth of tube, the tube 2.1–2.8 cm long, the lobes 0.5–1.0 cm long, puberulous outside, the lobes and abaxial surface of tube glandular-lepidote and puberulous inside, glandular-pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2.5–3 mm long, the longer filaments 1.4–1.7 cm long, shorter filaments 0.9–1.1 cm long, the staminode 4–5 mm long, inserted 6 mm from the base of the corolla tube; pistil 2.0–2.2 cm long, the ovary cylindric, 2–2.5 mm long and 1 mm wide, lepidote, the ovules 2-seriate; disc annular-pulvinate, 1.5 mm long and 2.5 mm wide. *Capsule* linear, 12–47 cm long, 1.6–2 cm wide, conspicuously glandular-pitted, the surface drying tannish-brown with the pits darker, midrib not visible, the margins slightly raised, more or less square-cornered; seeds

1.3–1.8 cm long and 3.6–5.2 cm wide, the wings hyaline-membranaceous at the tips, brown at the base, not sharply distinct from the seed body.

A plant of tropical dry forest and premontane moist forest, *Arrabidaea corallina* also occurs locally in tropical moist forest. In moist forests, this species is commonest along more or less exposed sandy or rocky shores where dry edaphic conditions seem to favor it. It ranges from Mexico to Argentina. This species flowers during the dry season from February to April.

Arrabidaea corallina is an extremely variable species. However, Central American specimens fall into two separable natural groups: Panamanian specimens have mostly glabrous leaves with conspicuous tufts in the vein axils beneath; Costa Rican specimens have strongly pubescent leaves and little development of tufts. Specimens from Mexico agree with the Costa Rican material. These two forms may prove to be at least varietally distinct despite the similarity of their flowers and fruits.

The large corolla and calyx of this species ally it with *Arrabidaea mollissima*, but it has a glabrous, pitted fruit as opposed to the evenly pubescent fruit of the latter. The pubescent form of *A. corallina* is distinguished from *A. mollissima* by its acuminate, more or less cuneate leaflets and the yellowish color of its pubescence and from the superficially similar *Xylophragma seemannianum* (O. Kuntze) Sandw. by its exclusively simple trichomes. The less pubescent form of *A. corallina* is similar to *A. florida* but differs in its tendency to round-tipped leaflets, and conspicuously barbate nerve axils.

CANAL ZONE: Near beach at Fort Kobbe, *Duke 4250* (MO). Farfan Beach, *Gentry 5500* (MO). LOS SANTOS: Las Tablas, *Dwyer 1179* (MO). PANAMÁ: Coronado Beach, *Croat 14258* (MO); *Gentry 752* (MO). Near archeological site at edge of Madden Lake, *Gentry 5007* (MO). Near Bejuco, *Miller 1793* (US). Gorgona beach, *Woodson et al. 1688* (A, MO, NY).

5. **Arrabidaea florida** DC., Prodr. 9: 184. 1845. TYPE: Brazil, Amazonas, *Martius s.n.* (G-DC, K, M).—FIG. 4A–C.

Vasconcellia florida Mart. *ex* DC., Prodr. 9: 184. 1845, pro syn.

Arrabidaea divaricata Bur. & K. Schum., Fl. Bras. 8(2): 33. 1896. TYPE: Peru, Tarapoto, *Spruce 4410* (K, NY).

Bignonia nitida Britton *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 34. 1896, pro syn. TYPE: Bolivia, Mapiri, *Rusby 1131* (MO, NY).

Arrabidaea panamensis Sprague, Bull. Herb. Boiss., sér. 2. 6: 371. 1906. TYPE: Panama, Canal Zone, *Hayes 735* (BM, K).

A. cardenasii Rusby, Mem. New York Bot. Gard. 7: 351. 1927. TYPE: Bolivia, Rurrenabaque, *Cardenas 2037* (NY).

Liana to 5 cm in diameter, the bark gray, inconspicuously longitudinally striate; stem with 4 phloem arms in cross section; branchlets terete, with raised warty lenticels, minutely scabrous when young, soon glabrate, without interpetiolar glandular fields; pseudostipules inconspicuous or lacking. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate to broadly ovate, acute to acuminate, broadly cuneate to truncate, more or less chartaceous, secondary nerves 4–7 on each side, beneath with scattered lepidote scales, above puberulous on the midvein, beneath puberulous on the main veins, drying olive green to olive gray, the terminal leaflet 8.5–14 cm long and 4.8–8.4 cm

wide; lateral leaflets 5–10.6 cm long and 4–6.3 cm wide; petiole and petiolules puberulous, terminal petiolule 0.9–2.6 cm long, lateral petiolules 0.5–2.7 cm long, petiole 0.9–6.2 cm long; tendril simple, 2.5–8 cm long. *Inflorescence* a terminal or axillary panicle of several to many dense trichotomous corymbs with long (1–5 cm) peduncles, its branches puberulous. *Flowers* sweetly aromatic, calyx cupular, 5-denticulate, 3–4 mm long and 2–3 mm wide, eglandular, simple-puberulous; corolla lavender with the tube white inside or white with purple filaments, abruptly campanulate, 1.2–1.7 cm long and 0.5–0.7 cm wide at the mouth of tube, the tube 0.7–1.2 cm long, the lobes 0.4–0.6 cm long, pubescent outside, on the lobes inside and on the bases of the stamens and staminode; stamens didynamous, subexserted, the anther thecae divaricate, 1.5 mm long, the longer filaments 0.8–0.9 cm long, the shorter filaments 0.5–0.7 cm long, the staminode 0.3–0.4 cm long, inserted 2–4 mm from the base of the corolla tube; pistil 0.8–1.0 cm long, the ovary linear-cylindric, 1–1.5 mm long, 0.5 mm wide, lepidote, the ovules 2-seriate; disc pulvinate, 1.0–1.5 mm long and 0.5 mm wide. *Capsule* linear, acuminate, compressed, 11–22 cm long and 0.9–1.0 cm wide, scattered lepidote, obscurely and minutely pitted, drying dark gray, the midrib and margins inconspicuously raised; seeds thin, bialate, 0.5–1.0 cm long and 2.3–3.6 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

Mostly occuring in tropical moist forest, also in premontane wet forest, this species is never common. It ranges from British Honduras to Bolivia. The plant flowers during the wet season from July to October (November).

Recognition of sterile plants is difficult, because of lack of noteworthy characters—no interpetiolar glands, no pseudostipules, tendrils not forked, leaves not noticeably pubescent. This species is vegetatively similar to *Adenocalymma apurense* (H.B.K.) Sandw. but lacks cartilaginous margins on the leaflets. It could also be confused with *Tynnanthus croatianus* A. Gentry which has trifid tendrils.

The typically short flowers of the Panamanian plants has led to their segregation as *Arrabidaea panamensis*. Since in all other characters, *A. panamensis* is identical with *A. florida* and size alone is an elusive character in this family, it is best to consider the Panamanian plants a form of *A. florida*, especially inasmuch as there is some overlap in the range of corolla size.

CANAL ZONE: Barro Colorado Island, *Aviles s.n.* (MO); *Bailey & Bailey 560* (GH); *Bangham 449* (A), *465*, pro parte (A, F), *465A* (A); *Chickering 59* (F); *Croat 11122* (MO, NY, SCZ), *11798* (MO, SCZ), *12647* (MO); *Foster 1081* (PMA), *1338* (MO); *Shattuck 1036* (F, MO); *Starry 149* (F, MO). Vicinity of Gamboa, *Allen 1968* (F, MO, NY, US). Gaillard Highway 2 mi. NW of Summit Garden, *Croat 11893* (MO, SCZ). Along old Gamboa road between Summit Hills Golf Course and Summit Radio Station, *Croat 16664* (MO). Pipeline Road, D'*Arcy 6019* (C, MO, PMA, UCWI); *Gentry 1430, 4787, 5065* (all MO). Across from Summit Hills Golf Course, *Gentry 1588, 1605, 2818* (all MO), *1774* (MO, SCZ). Río Grande Station, Panamá Railroad, *Hayes 735* (BM, K). Farfan Beach road, *Kirkbride & Elias 60* (MO, NY, SCZ). DARIÉN: Vicinity of Boca de Cupe, *Allen 909* (F, GH, MO, NY, US). Río Balsa between Quebrada Chusomocatre and Río Aretí, *Duke 8707* (MO). Río Piñas, *Duke 10577* (MO). Río Tuira between Ríos Punusa and Mangle, *Duke 14577* (MO). Shore near Majagualito across from La Palma, *Gentry 3990* (MO). Above Jaqué, *Gentry 4176* (MO). S of Jaqué, *Gentry 4279* (MO). Río Paya from Río Tuira to village of Paya, *Gentry 4388* (MO). PANAMÁ: Entrado a Nuevo Emperador cerca de Arraiján, *Bakes 11* (MO, PMA);

Castillo 14 (MO); *Guerra 11* (PMA). Cerro Campana above Su-Lin Motel, *Gentry 1844* (MO). Río Tatare, *Woodson & Schery 1017* (GH, MO) . WITHOUT LOCALITY: *Bristan 746* (MO).

6. **Arrabidaea mollissima** (H.B.K.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 46. 1896.

Bignonia villosa Vahl, Eclog. Amer. 2: 44. 1798, pro parte. TYPE: Colombia, Magdalena, *von Rohr 21* (C, leaves only).
B. mollissima H.B.K., Nov. Gen. Sp. Pl. 3: 133. 1819. TYPE: Venezuela, Valles de Aragua, *Humboldt & Bonpland 740* (P).
B. littoralis H.B.K., Nov. Gen. Sp. Pl. 3: 139. 1819. TYPE: Mexico, Guerrero, *Humboldt & Bonpland 3860* (P).
Panterpa mollissima (H.B.K.) Miers, Proc. Roy. Hort. Soc. 3: 196. 1863.
Bignonia acapulcensis H.B.K. *ex* Baill., Hist. Pl. 10: 28. 1888, pro syn.
Arrabidaea mollicoma Blake, Contr. Gray Herb. 52: 92. 1917. TYPE: Nicaragua, La Paz, *Baker 2268* (GH, MO, US).
A. seleriana Loes., Verhandl. Bot. Verein Prov. Brandenburg 65: 99. 1923. SYNTYPES: Guatemala, Chiquimula, *Seler 3348* (GH); Mexico, Oaxaca, *Seler 1621* (not seen).
A. isthmica Standl., Jour. Washington Acad. Sci. 15: 461. 1925, pro parte. TYPE: Panama, Canal Zone, *Pittier 2576* (flowers only) (GH, MO, NY, US).
A. littoralis (H.B.K.) Standl., Contr. U. S. Natl. Herb. 23: 1318. 1926.
A. guaricensis Pittier, Jour. Washington Acad. Sci. 18: 337. 1928, pro parte. TYPE: Venezuela, Guarico, *Pittier 11308* (flowers only) (GH, US, VEN).
A. sanctae-marthae Sprague *ex* Sandw., Recueil Trav. Bot. Néerl. 34: 229. 1937, nomen nudum. TYPE: Colombia, Magdalena, *Smith 743* (BR, K, MO, NY).

Liana to 3 cm in diameter, the bark smooth, gray; stem with 4 phloem arms in cross section; branchlets terete, glabrate, usually with interpetiolar glandular fields, at least at some nodes; pseudostipules small, inconspicuous, narrow and pointed. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar, deciduous during the dry season; leaflets broadly ovate to subrotund, more or less obtuse, the base rounded or truncate, 3.9–9.3 cm long and 2.4–7.0 cm wide, membranaceous, secondary veins 4–5 on each side, scattered lepidote scales on each side, strongly pubescent with long simple trichomes, especially along main veins, ciliate, rarely much less pubescent or glabrate, drying olive to brownish olive, tendril simple, 8–9 cm long; petiolules 0.5–2.5 cm long, the petiole 2–3.7 cm long, pubescent as the petiolules. *Inflorescence* a large terminal panicle of a series of axillary panicles, its branches pubescent. *Flowers* fragrant, calyx cupular, 5-denticulate, 4–7 mm long and 3–6 mm wide, puberulous with simple trichomes, the margin ciliate with whitish simple trichomes, usually with a few scattered glands; corolla lavender outside and on the lobes inside, the tube white inside with a yellow spot on the roof of corolla over anthers, occasionally wholly white; tubular-campanulate, 2.5–5.3 cm long and 0.8–1.6 cm wide at the mouth, the tube 1.8–3.6 cm long, the lobes 0.6–1.2 cm long; moniliform-pubescent outside and on margins of lobes, simple pubescent inside with multicellular trichomes on lobes and with 1–3-celled, gland-tipped trichomes at and just below the level of stamen insertion and on the floor of the tube; stamens didynamous, the anther thecae divaricate, 4–5 mm long, the longer filaments 1.5–1.7 cm long, the shorter filaments 1.1–1.2 cm long, the staminode 1–2 mm long, inserted 5–7 mm from base of corolla tube; pistil 2–2.1 cm long, the ovary tapered-cylindric, 3 mm long, 1 mm wide, glandular-puberulous or

lepidote, the ovules 2-seriate in each locule; disc pulvinate, 1 mm long 2 mm wide. *Capsule* linear, 14.5–17 cm long, 1.2–1.5 cm wide, softly pubescent, drying brownish, the midrib inconspicuous but sometimes slightly raised; seeds thin, 1.1–1.4 cm long and 3.6–4.3 cm wide, bialate, the wings hyaline-membranaceous.

Restricted to tropical dry forest and drier parts of the premontane moist forest and tropical moist forest. *A. mollissima* is common in Guanacaste Province, Costa Rica, and sporadic along the Pacific slope from Mexico to Venezuela. The species flowers during the dry season from late January to early March. Deciduous during the blooming period, its lavender flowers often cover a leafless dry forest tree creating a spectacular appearance similar to a flowering tree of *Tabebuia impetiginosa*.

The round pubescent leaves with conspicuously ciliate margins are a good field character. Its relatively large corolla and calyx separate *A. mollissima* from other Central American species of *Arrabidaea* except *A. corallina* from which it is most easily distinguished by its soft-pubescent fruit. A white-flowered form is clearly conspecific and does not merit formal recognition.

Confusion surrounds the name *A. littoralis*, which Standley apparently used as a catch-all for anything close to *Arrabidaea* which he could not otherwise name. *Arrabidaea littoralis* as determined by Standley in various herbaria includes such diverse elements as *Clytostoma binatum* (*Haenke 1022*), *Pachyptera alliacea* (*Haenke 1518*), *Arrabidaea costaricensis* (*Molina 2725*), *A. corallina* (*Standley 40042*, *Williams & Molina 12581*), *A. pubescens* (*Kenoyer A348*), *A. patellifera* (*Palmer 362*, pro parte), and *A. mollissima* (*Edwards P-577*).

CANAL ZONE: Road K-10, *Duke 15193* (MO). Near junction Gamboa Road, *Harvey 5242* (F). Chiva Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5751* (US). Río Agua Salud near Corozal, *Piper 5855* (US). Vicinity of El Paraíso, *Pittier 2576*, pro parte (GH, MO, US). Near Corozal Hospital, *Wetmore & Abbe 276* (A). Ancón Hill, *Williams 14* (US). COCLÉ: Mountains beyond La Pintada, *Hunter & Allen 510* (K, MO, US), *511* (MO, NY, P). Penonomé and vicinity, *Williams 83* (NY, US), *427* (NY), *428* (US). DARIÉN: Punto Sabanas opposite La Palma, *Gentry 3951*, *3956* (both MO). Punta Patiña NNE of Garachiné, *Gentry 4052* (MO). PANAMÁ: Along road to Pacora, *Allen 841* (K, MO, P, US). Río Las Lajas, *Allen 1602* (MO). Vicinity of Arraiján, *Allen 1623* (F, GH, MO, NY, US). Vicinity of Bejuco, *Allen 4202* (F, MO). Río Pasiga, *Gentry 2268* (MO). Icantí, *Gentry 2605* (MO). Trail from Río Espavé toward Río Agua Clara, *Gentry 3777* (MO). 0–4 km from Bayano crossing on road to Santa Fé, *Gentry 3860* (MO). Along road to Cerro Azul, *Gentry 4896* (MO). E of Cañitas, *Gentry 4974* (MO). Road to Cerro Azul, *Gentry et al.* 3393 (MO). Punta Paitilla, *Piper 5395* (US). Between Matías Hernándes and Juan Díaz, *Standley 32055* (K, US). VERAGUAS: 6 mi. S of Santa Fé, *Gentry 2932* (MO).

7. **Arrabidaea oxycarpa** Urb., Feddes Repert. 14: 301. 1916. TYPE: Trinidad, *Broadway 3188* (not seen).

Vine, the branchlets terete, lepidote to slightly puberulous, when young drying black with contrasting whitish lenticels, without interpetiolar glandular fields; pseudostipules small, blunt, inconspicuous. *Leaves* 3-foliolate or 2-foliolate with a simple tendril, the blade elliptic, somewhat acuminate, rounded to broadly cuneate at base, 3–12 cm long and 1–6 cm wide (smaller at base of branchlet), chartaceous (usually immature and membranaceous when in flower), slightly

lepidote, otherwise glabrous except for simple trichomes in axils of lateral nerves beneath, drying lead gray to blackish, the main veins darker beneath, the ultimate venation intricately reticulated; petiolules 0.2–3 cm long, the terminal longer, laterals shorter, petiole 1.5–5 cm long, lepidote, drying black. *Inflorescence* a reduced, few-flowered panicle terminal on young lateral branchlets, its branches lepidote and puberulous, drying blackish, bracts minute. *Flowers* with the calyx cupular, 3–4 mm long and 3–4 mm wide, evenly but minutely 5-denticulate, lepidote and puberulous, usually with conspicuous plate-shaped glands near margin, drying dark; corolla magenta, tubular campanulate, 3–3.5 cm long and 1.3–1.4 cm wide, the tube 2.2–2.4 cm long, the lobes ca. 1 cm long, densely puberulous without and on lobes within, the trichomes somewhat glandular, the tube inside glabrous except for trichomes at base of stamens; stamens didynamous, the anther thecae divaricate, 3 mm long, the connective slightly extended, the longer filaments 1.6–1.7 cm long, the shorter filaments 1.2–1.3 cm long, the staminode 6–7 mm long; inserted 5 mm from base of corolla tube; pistil 1.6–1.7 cm long, the ovary linear oblong, 2–3 mm long and 1 mm wide, minutely lepidote, the ovules 2-seriate in each locule; disk pulvinate, 1 mm long and 1.5–2 mm wide. *Capsule* linear, compressed, tapered at both ends, 19–23 cm long and 1 cm wide, drying brown or blackish, glabrous or slightly lepidote, the midrib evident but slightly raised and inconspicuous, the margins somewhat raised; seeds thin, flat, bialate, 0.7–0.8 cm long and 1.7–2.8 cm wide, the wings sharply divided into a brown basal part and a hyaline membranaceous tip.

An uncommon vine of the premontane moist forest and edaphically dry areas of the tropical moist forest, *A. oxycarpa* has been previously known only from Trinidad.

I have seen only a single specimen of this species from Trinidad. However, I have recently examined a series of specimens from Venezuela which I would identify with *A. oxycarpa* and am now convinced that two fruiting collections from the Canal Zone which I had tentatively identified with *A. florida* are actually *A. oxycarpa*. *Arrabidaea oxycarpa* differs from *A. florida* in mature branchlets with a loose, inconspicuously lenticellate, somewhat wrinkled epidermis in contrast to the tight, unwrinkled, uniformly small-lenticellate epidermis of the latter. The leaves of *A. oxycarpa* also tend to dry a darker gray with a more intricate pattern of ultimate reticulations below. In flower *A. oxycarpa* is characterized by young branchlets which dry blackish with conspicuous light lenticels and by its reduced, few-flowered inflorescences.

CANAL ZONE: Boy Scout Camp Road near Madden Lake, *Gentry 5504* (MO). Farfan Beach Road, *Kirkbride & Elias 60* (MO, NY, SCZ).

8. **Arrabidaea patellifera** (Schlecht.) Sandw., Kew Bull. 22: 413. 1968.

Bignonia patellifera Schlecht., Linnaea 8: 516. 1833. TYPE: Mexico, Hacienda de la Laguna, *Schiede & Deppe 153* (BM, MO).
B. cupulata Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 6. 1842. TYPE: Brazil, Para (not seen).
Tabebuia neurophylla Miq., Linnaea 26: 219. 1853. TYPE: Surinam, *Kappler 1957* (C, U).
Petastoma patelliferum (Schlecht.) Miers, Proc. Roy. Hort. Soc. 3: 195. 1863.
Arrabidaea pentstemonoides Kränzl., Notizbl. Bot. Gart. Berlin 6: 370. 1915. TYPE: Brazil, Rio Acre, *Ule 9780* (K).

Cuspidaria mollis Kränzl., Notizbl. Bot. Gart. Berlin 6: 376. 1915. TYPE: (not seen).
Petastoma broadwayi Sprague & Riley, Kew Bull. 1921: 311. 1921. TYPE: Trinidad, *Broadway 4164* (K, NY).
P. breviflorum Standl., Jour. Arnold Arbor. 11: 128. 1930. TYPE: Panama, Barro Colorado Island, *Bangham 465*, pro parte (A, F).
P. domatiatum Sampaio, Bol. Mus. Nac. Rio de Janeiro 12: 87. 1931. TYPE: Brazil, Amazonas, *Ducke 24089* (K).
P. pentstemonoides (Kränzl.) Sandw., Kew Bull. 43: 7. 1959.
Arrabidaea broadwayi (Sprague & Riley) Sandw., Kew Bull. 22: 414. 1968.

Liana to at least 5 cm in diameter, the bark light gray; stem with 4 phloem arms in cross section; branchlets light gray or brown usually with raised whitish lenticels, glabrous to lepidote or scabrous, the nodes without interpetiolar glandular fields, often with a ridge connecting opposite petioles; pseudostipules usually lacking, when present foliaceous, small, soon deciduous. *Leaves* simple or 2-foliolate, sometimes with a tendril; leaflets (or leaf blades) ovate to rhombic-ovate, sometimes serrate, acuminate to obtuse, broadly cuneate to rounded 4.7–14.5 cm long and 2.9–10.5 cm wide, membranaceous, the secondary veins 4–6 on a side, the basal nerves often making more acute angle with midvein than upper nerves, somewhat lepidote above and beneath, conspicuously simple-puberulous beneath mostly on the nerves, less so above (rarely glabrate, *e.g. Gentry 1955*), drying more or less olive, the pubescent veins lighter beneath; tendril simple, 4–16 cm long; petiole and petiolules conspicuously pubescent with long simple trichomes, petiolules 0.5–2.2 cm long and petiole 0.7–1.9 cm long in compound leaves, petiole 1.1–3.5 cm long in simple leaves. *Inflorescence* an axillary or terminal, usually many-flowered panicle, the branches puberulent and lepidote, the buds appearing conspicuously white-tipped from the pubescent corolla lobes. *Flowers* sweetly aromatic, calyx open, patelliform, more or less truncate, 1–4 mm long and 4–8 mm wide, scattered lepidote and simple-pubescent, glands absent; corolla magenta, the throat usually white with magenta ridges, sometimes wholly magenta, campanulate above the narrowed base, 2.2–4.3 cm long and 0.5–1.7 cm wide at the mouth, the tube 1.4–2.6 cm long with basal constriction 0.5–0.8 cm long, the lobes 0.4–1.2 cm long; the tube glabrate outside with occasional widely scattered lepidote scales or simple trichomes, the lobes densely simple pubescent, tube glabrous inside except for gland-tipped trichomes at the level of stamen insertion; stamens didynamous, anther thecae divaricate, bent forward slightly, 1.5–2 mm long, the longer filaments 1.1–1.3 cm long, the shorter filaments 0.8–1.0 cm long; the staminode 3–4 mm long, inserted 5–7 mm above the base of the corolla tube; pistil 1.5–2.3 cm long, the ovary linear, 1.5–2.5 mm long and 0.5–1 mm wide, slightly lepidote, the ovules 2-seriate; disc annular-pulvinate, 0.5–1 mm long and 1.5–2 mm wide. *Capsule* linear, acute, flattened, 11–39 cm long and 0.9–1.4 cm wide, the midrib appearing as a slightly raised line, the surface generally minutely papillose and smooth, rougher on the slightly raised margins with a few scattered trichomes and lepidote scales; seeds 0.7–1.0 cm long and 2.5–3.9 cm wide, the wings membranaceous with hyaline ends distinct from the brown bases, the wing bases not demarcated from the seed body.

A widespread liana common in the tropical dry forest and premontane moist

forest, it becomes less common in tropical moist forest and rare in tropical wet forest. It ranges from Mexico to Brazil. This species flowers during the wet season from June to November, also rarely and irregularly in January or February. The wind-dispersed seeds are released in mid dry season.

Useful vegetative charcters are the typically strongly pubescent main veins beneath, the pubescent petioles and petiolules, and the frequent simple leaves. The sharp angle of the basal lateral veins with the midvein is another diagnostic character. The reflexed patelliform calyx and white-tipped bud are distinctive, but the fruit is similar to that of several other species of *Arrabidaea*.

Petastoma breviflorum is no more than a form with atypically short corollas; while I have seen no other specimens of *A. patellifera* with such short corollas, intensive collecting on Barro Colorado Island has turned up no additional material of this sort. Even greater variation in corolla length is well documented within other species of Bignoniaceae, even on the same plant.

Both the segregating characters (larger calyx and less pubescent or almost glabrous leaves) of *Arrabidaea broadwayi* from Trinidad are within the range of variation of *A. patellifera*. Also falling into this category are *P. domatiatum* and *A. pentstemonoides*. *Arrabidaea patellifera* itself is close to *A. samydoides* (Cham.) Sandw. of Brazil. Should they prove synonymous, the Brazilian name would have to be adopted.

CANAL ZONE: Barro Colorado Island, *Aviles 118, 889* (both F); *Bailey & Bailey 280* (F, GH); *Bangham 465* (A, F), *553* (A); *Croat 5222* (NY, SCZ), *6065* (MO, SCZ), *6654, 6724, 9794, 10895* (all MO), *11126* (F, MO, NY, SCZ), *13161* (MO, SCZ), *13244A, 15144* (both MO); *Dodge & Woodworth 3506* (GH, NY, US); *Ebinger 276* (MO, US); *Foster 1024* (MO, PMA), *1338B* (MO); *Kenoyer 531* (US); *Shattuck 258* (A, F, MO), *300* (F, MO), *889* (MO); *Starry 202* (F, MO); *Wetmore & Abbe 71* (A, F, MO), *163* (A, F, MO); *Wetmore & Woodworth 78* (F); *Woodson & Schery 970* (GH, MO); *Woodworth & Vestal 360* (MO). Near water reservoir W of Cocoli, *Croat 9162* (MO, SCZ). Ancon Hill, *Duke 4606* (K, MO). Pipeline road, *Gentry 1585, 1955* (both MO). Road K-10, *Gentry 1961* (MO, SCZ). Between Corozal and Ancón, *Pittier 6771* (NY, US). Balboa, *Standley 26991* (MO, US). Vicinity of Miraflores near mouth of Cocoli River, *White 128* (GH, MO). Fort Kobbe road, *Woodson et al. 1416* (A, MO, NY). CHIRIQUÍ: Trail from San Félix to Cerro Flor, *Allen 1918* (MO). E of Gualaca, *Allen 5031* (MO). DARIÉN: Río Chica vicinity of Yaviza, *Allen 4577* (F, K, MO, P, US). Between Quebrada Venado and Peje swamp on headwaters of Río Tuqueza, *Bristan 1054* (F, MO, NY). Río Ucurgantí, *Bristan 1156* (MO). Tumagantí, *Duke 14146* (MO, SCZ). Trail to Cerro Pirre, *Gentry 4608* (MO). HERRERA: Road from La Arena to Pesé, *Burch et al. 1284* (MO). Road between Las Minas and Pesé, *Duke 12333* (MO). E of Las Minas, *Gentry 3136, 3141, 3147* (all MO). PANAMÁ: Vicinity of Arraiján, *Allen 1621* (F, GH, MO, NY, US). SE part of Gatun Lake near Río Pescado, *Bartlett & Lasser 16595* (MO). Río Charco-Espiritu on Tocumen Highway, *Duke 5703* (MO, SCZ). Bald savanna-like areas along road toward top of Cerro Campana, *Duke 5977* (GH, MO). Río Maestro, *Gentry 2234* (MO). Río Pasiga, *Gentry 2351* (MO). Near Río Espavé, *Gentry 3707* (MO). Chimán, *Lewis et al. 3352* (MO, SCZ). Cerro Campana, *McDaniel 6811A* (MO). Río Tapia, *Standley 28131* (US). VERAGUAS: Santiago toward Atalaya, *Dwyer & Kirkbride 7401* (GH, K, MO, US). 2 mi. W of Santiago, *Dwyer et al. 7559* (MO). S of Santa Fé, *Gentry 2936* (MO). Vicinity of Santiago, *Stern et al. 997* (GH, MO). 2 mi. S Cañazas, *Tyson 3729* (MO).

9. **Arrabidaea pubescens** (L.) A. Gentry. Brittonia 25: 239. 1973.

Bignonia pubescens L., Sp. Pl., ed. 2. 2: 870. 1763. TYPE: Mexico, Campeche, *Houstoun s.n.* (not seen).

Arrabidaea blanchetii DC., Prodr. 9: 186. 1845. TYPE: Brazil, Bahia, *Blanchet 2363* (G-DC).

A. pleei DC., Prodr. 9: 184. 1845. TYPE: Venezuela, Maracaibo, *Plée 89* (G-DC, K, P, US).
A. sieberi DC., Prodr. 9: 186. 1845. TYPE: Trinidad, *Sieber 109* (G-DC, GH).
Petastoma pubescens (L.) Miers, Proc. Roy. Hort. Soc. 3: 195. 1863.
Arrabidaea carabobensis Pittier, Jour. Washington Acad. Sci. 18: 335. 1928. TYPE: Venezuela, Carabobo, *Pittier 7915* (VEN).
A. lundellii Standl., Publ. Field Mus. Bot. 8: 48. 1930. TYPE: British Honduras, Orange Walk, *Lundell 56* (F, holotype; US, isotype).

Liana to 2.5 cm in diameter, stem with 4 phloem arms in cross section; branchlets terete, puberulous with interpetiolar glandular fields; pseudostipules inconspicuous or lacking. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate, acute to acuminate, rounded to broadly subcordate at base, 4.5–13 cm long and 2.5–8 cm wide, membranaceous, secondary nerves 4–5 on a side, palmately 3–5-veined from base, densely short-puberulous beneath, above puberulous with extremely short trichomes to glabrate with scattered trichomes, drying olive to brown above, tan beneath, the veins pubescent beneath and colored about the same as the surface; tendril simple, 5–7 or more cm long; petiolules 0.8–1.8 cm long, petiole 1.7–3.1 cm long, densely short-puberulous. *Inflorescence* an axillary panicle, its branches puberulous. *Flowers* with the calyx cupular, truncate, minutely 5-denticulate, 3 mm long and 2–3 mm wide, puberulous, usually with some glands; corolla lavender, campanulate, 1.3–1.8 cm long and 0.5-0.7 cm wide at the mouth, the tube 0.8–1.1 cm long, the lobes 0.3–0.5 cm long, the tube pubescent outside, abaxially pubescent inside and at the level of stamen insertion, the lobes puberulous; stamens didynamous, the anther thecae divaricate, 2 mm long, the longer filaments 0.9–1.0 cm long, the shorter filaments 0.6–0.8 cm long, the staminode 2–4 mm long, inserted 2–4 mm from base of corolla tube; pistil 1.0–1.1 cm long, the ovary oblong, densely lepidote, 1.5 mm long and 0.5–1 mm wide, the ovules 2-seriate; disc pulvinate, 1 mm long and 1–1.5 mm wide. *Capsule* linear, acuminate, compressed, 7.2–8.8 cm long and 0.6–0.8 cm wide, lepidote, drying dark brown, the midline and margins slightly raised; seeds thin, bialate, 5 mm long, 1.4–1.5 cm wide, the wings hyaline-membranaceous, distinct from the dark brown seed body.

A plant mainly of the tropical dry forest, *A. pubescens* is widely distributed from Tamaulipas, Mexico, to Brazil, mostly near the coast. It flowers during early and mid-wet season from June to August.

The complex synonymy of this species is discussed elsewhere (Gentry, Brittonia 25: 238–239. 1973).

CANAL ZONE: Farfan Beach Road, *Gentry & Dwyer 3545* (MO). COCLÉ: Between Aguadulce and Antón, *Woodson et al. 1224* (A, K, MO, NY). DARIÉN: Punta Patiño NNE of Garachiné, *Gentry 4042* (MO). Near Punta Alegre NE of Garachiné, *Gentry 4060* (MO). PANAMÁ: Río Las Lajas, *Allen 3613* (F, GH, K, MO, NY, U, US). Mouth of Río Pasiga, *Gentry 2201* (MO). Near Panamá, *Hayes 93* (BM, K). Gorgona Beach, *Woodson et al. 1689* (A, MO, NY). Taboga Island, *Gentry 5713* (MO), *Woodson et al. 1489* (A).

5. CALLICHLAMYS

Callichlamys Miq., Linnaea 18: 254. 1844. TYPE: *C. riparia* Miq. = *C. latifolia* (L. C. Rich.) K. Schum.

Lianas, but shrubby when young, stems with 4 phloem arms in cross section; branchlets terete without interpetiolar glandular fields; pseudostipules lacking. *Leaves* 3-foliolate, the terminal leaflet sometimes replaced by a simple tendril. *Inflorescence* a short axillary (rarely terminal), 1–12-flowered raceme. *Flowers* with the calyx of a thick spongy material, inflated-cupular, irregularly lobed; corolla large, infundibuliform-campanulate, the tube contracted above the ovary, sparsely and inconspicuously glandular-lepidote outside; anthers glabrous, the thecae straight, divaricate; pollen grains 3-colpate, microreticulate; ovary ovate-cylindric, narrowed slightly at the base, more or less glabrous, the ovules 4–8-seriate in each locule; disc annular-pulvinate. *Fruit* an oblong-elliptic or oblong capsule, the valves parallel to the septum, compressed, woody, smooth; seeds large, thin, the wings brown, not demarcated from the seed body.

One species ranging from Mexico to Brazil.

Callichlamys latifolia (L. C. Rich.) K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 223. 1894.—FIG. 5.

Bignonia latifolia L. C. Rich., Act. Soc. Hist. Nat. Paris 1: 110. 1792. TYPE: French Guiana, Rio Kourou, *Le Blond s.n.* (P).
B. hondensis H.B.K., Nov. Gen. Sp. Pl. 3: 135. 1819. TYPE: Colombia, Honda, *Humboldt & Bonpland 1706* (P).
Tabebuia latifolia (L. C. Rich.) DC., Rev. Bign. (Bibl. Univ. Genève) 15. 1838.
Delostoma latifolia (L. C. Rich.) Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 11. 1842.
Callichlamys riparia Miq., Linnaea 18: 254, 609. 1844. TYPE: Based on *Bignonia latifolia* L. C. Rich.
Bignonia crucifera Bert. *ex* DC., Prodr. 9: 213. 1845, pro syn.
Tabebuia rufinervis DC., Prodr. 9: 213. 1845. SYNTYPES: Colombia, Santa Marta, *Bertero s.n.* (G-DC, M); British Guiana, *Schomburgk 575* (F, G-DC); Brazil, Pará, *Sieber s.n.* (not seen); Rio de Janeiro, *Luschnath s.n.* (not seen).
T.? mansoana DC., Prodr. 9: 214. 1845. TYPE: Brazil, Cujaba, *Manso s.n.* (G-DC).
Lundia schomburgkii Kl. *in* Schomburgk, Reisen 2: 1158. 1848, nomen nudum.
Callichlamys rufinervis (DC.) Miers, Proc. Roy. Hort. Soc. 3: 201. 1863.
C. rubiginosa Miers, Proc. Roy. Hort. Soc. 3: 201. 1863, nomen nudum. TYPE: Brazil, Organ Mountains, *Miers s.n.* (not seen).
Callichlamys splendida Miers, Proc. Roy. Hort. Soc. 3: 201, nomen nudum. TYPE: Brazil, Rio de Janeiro, *Cunningham s.n.* (not seen).
C. peckoltii Bur. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 223, *fig. 88M–N*. 1894. SYNTYPES: Brazil, Rio de Janeiro, *Peckolt 533* (BR); *Peckolt 592* (not seen).
Tabebuia speciosa Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 49. 1930. TYPE: British Honduras, Middlesex, *Schipp S-51* (F).
Callichlamys garnieri Standl. & L. O. Wms., Ceiba 3: 130. 1952. TYPE: Nicaragua, Managua, *Garnier 130* (F).

Liana to 7.5 cm in diameter, the bark light gray, smooth with scattered raised whitish lenticels; stem with 4 phloem arms in cross section; twigs sub-terete, light gray with large, widely scattered raised lenticels, the nodes without interpetiolar glandular fields, interpetiolar ridges, or noticeable pseudostipules. *Leaves* 3-foliolate or 2-foliolate with a tendril or an inconspicuous tendril scar; leaflets elliptic, acuminate, broadly cuneate to rounded, membranaceous to chartaceous, secondary veins 5–9 on a side, minutely papillose above and beneath with scattered lepidote scales, these sometimes deciduous above, pubescent beneath in the axils of lateral nerves, usually subpuberulous on main veins with simple and stellate trichomes, sometimes conspicuously dendroid

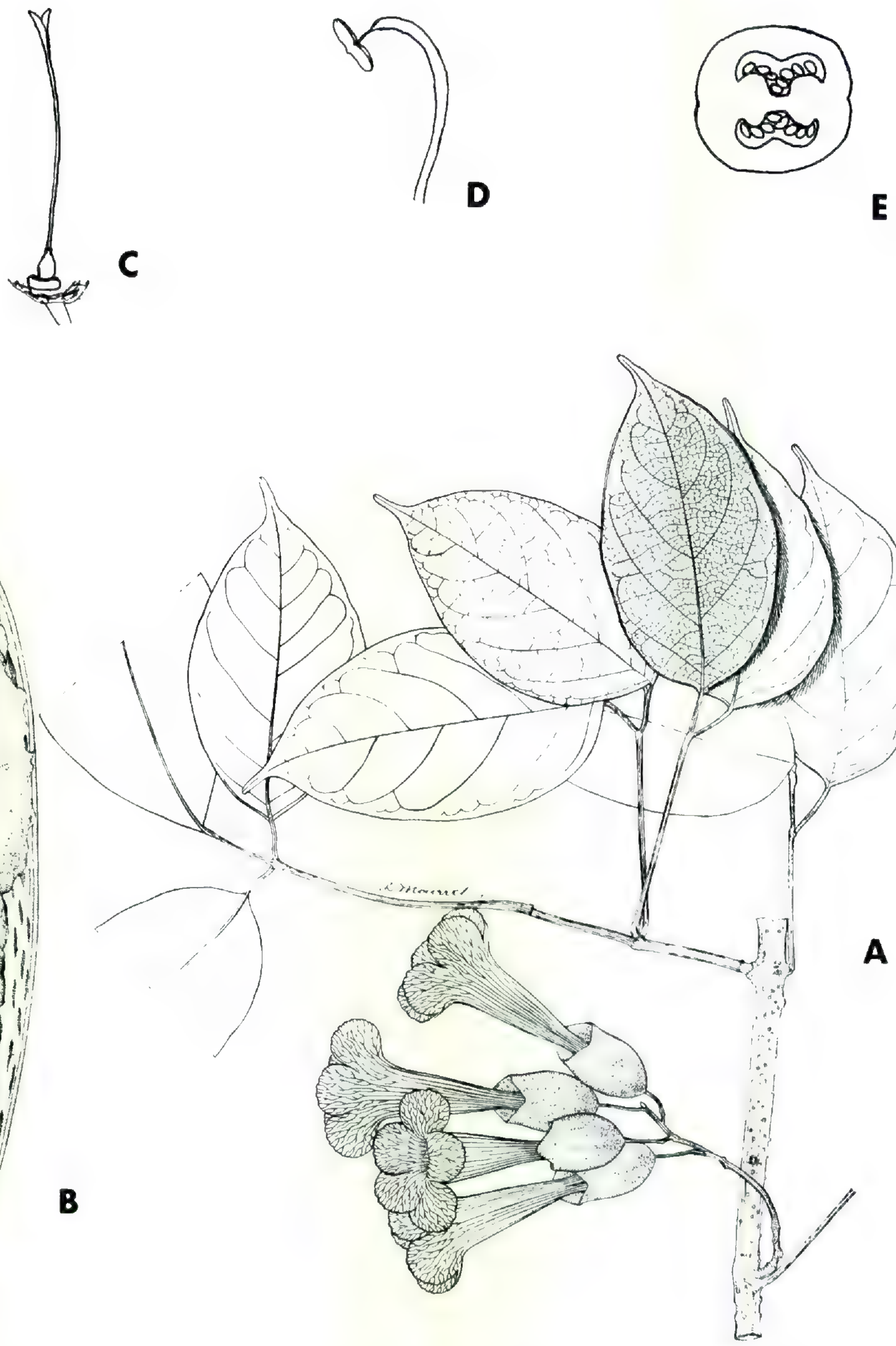

FIGURE 5. *Callichlamys latifolia* (L. Rich.) K. Schum.—A. Habit (× ½). [After *Gentry 1896* (MO).]—B. Fruit (× ½). [After *Croat 8058* (MO).]—C. Pistil and disc (× ⅗).—D. Stamen (× 3).—E. Ovary cross section (× 6). [After *Gentry 1777* (MO).]

pubescent on the undersurface, with plate-shaped glands along the midvein, mostly in axils of the lateral nerves, drying green to olive with the main nerves yellowish or contrastingly reddish, the terminal leaflet 9.5–37 cm long and 4.2–22 cm wide, the lateral leaflets 7–31 cm long and 3.4–18 cm wide; terminal petiolule 1.8–9.5 cm long, lateral petiolules 1.1–4.8 cm long, petiole 2.5–18 cm long, glabrous to minutely scabrous as the petiolules; tendril simple 9–20 cm long.

Inflorescence a short terminal or axillary, 1–12-flowered raceme, the pedicels 1–1.5 cm long, each with 2 narrow bracts, the rachis to 8 cm long, the rachis and pedicels sparsely stellate-puberulent. *Flowers* with an inconspicuous sweetish musky odor, calyx large, yellow when fresh, spongy, inflated-campanulate, more or less bilabiate, mostly glabrous with scattered plate-shaped glands, sparsely and inconspicuously thick-stellate and/or simple puberulent near the base, or rarely conspicuously stellate pubescent, 2.2–6.0 cm long and 1.2–4.2 cm wide; corolla bright yellow with red penciling in the throat (13 lines), tubular-campanulate, 5.5–11 cm long and 1.3–2.8 cm wide at the mouth, the tube 4.5–7.5 cm long, the lobes 1.2–3.2 cm long; sparsely and inconspicuously lepidote inside and out, glandular-pubescent inside from the level of stamen insertion to the top of the enlarged base; stamens didynamous, the anther thecae divaricate, 2–3 mm long, the filaments abruptly narrowed for the apical 2 mm, the longer pair 2.5–3.8 cm long, the shorter pair 1.5–2.3 cm long, the staminode 0.6–1.1 mm long, inserted 1.2–2.0 cm from base of corolla tube; pistil 5.2–5.7 cm long, the ovary ovate-cylindric, 3–4 mm long and 2.5–3.5 mm wide, narrowed slightly at the base, essentially glabrous, the ovules 8-seriate in each locule; disc annular-pulvinate, 2 mm long and 6–7 mm wide. *Capsule* oblong or elliptic-oblong, obtuse at the ends, the valves woody, flattened, 24–32 cm long and 6.0–11.5 cm wide, the surface smooth, glabrous with a wrinkled epidermis, drying blackish with scattered lighter inconspicuous lenticellate spots; seeds 2.5–4.3 cm long and 6.7–13 cm wide, the wings brown, thinly woody at the base to submembranaceous at the tips, not distinct from the seed body.

Widespread in tropical moist forest and tropical wet forest, but seldom abundant, this plant ranges from Mexico to Brazil, flowering mostly toward the end of the wet season in October and November but sporadically throughout the year.

The plant is characterized by large leaflets which have conspicuous tufts of dendroid trichomes in the axils of the lateral nerves beneath. The smooth gray bark with whitish lenticels is another field character. On drying, the leaves can usually be recognized by the red-drying main veins. The large flat fruit is almost unmistakable.

A second species of *Callichlamys*, *C. garnieri* Standl. and L. O. Wms., has recently been described from Nicaragua. This is known only from the type and was differentiated from *C. latifolia* mainly on the basis of a larger flower and strongly pubescent leaves and calyx. It is a pubescent variant of *C. latifolia*. Another pubescent variant was described by De Candolle as *Tabebuia mansoana*.

BOCAS DEL TORO: Mountains above Almirante, *Gentry 2734*, *2812* (both MO). CANAL ZONE: Barro Colorado Island, *Aviles 16B* (F, MO); *Croat 6819* (MO, NY, SCZ), *6835* (MO), *6854A* (MO, NY, SCZ), *8058* (MO, NY, SCZ); *Foster 1383* (MO, PMA); *Shattuck 361* (F, MO). Near Río Gatuncillo, *Allen 5137* (MO). S of Pedro Miguel Locks, *Croat 9173* (MO, SCZ). Madden Lake, *Gentry 702* (F, MO), *703* (MO). Madden Forest, *Gentry 1383* (MO). Pipeline Road, *Gentry 1581* (MO). Road K-19, *Gentry 1777* (MO, SCZ). Road K-10, *Gentry 1896* (MO, SCZ). Boy Scout Road near Madden Lake, *Gentry 2073* (MO). Empire Station, Panama Railroad, *Hayes 248* (BM, K, P, W). N of Paraíso, *Lazor & Blum 5319* (SCZ). Near Contractor's Hill, *Lewis et al. 2880* (MO, NY, SCZ). COLÓN: Santa Rita Ridge, *Dressler 3513* (PMA); *Gentry 461* (MO). DARIÉN: Río Balsas above Río Aretí, *Duke 8710* (MO). S of

Jaqué, *Gentry 4106* (MO). Above Río Clarita on Río Tuira, *Gentry 4322* (MO). Río Tuira near Río Paya, *Gentry 3378* (MO). Río Tuira between Ríos Paya and Espavé, *Gentry 4421* (MO). Summit of Cerro Pirre, *Gentry 4617* (MO). PANAMÁ: Near Vigía and San Juan on Río Pequení, *Dodge et al. 16519* (BM, C, K, MO, P, U). Dam site at Río Bayano, *Gentry & Tyson 1662* (MO). Río Pasiga, *Gentry 2200, 2258, 2309, 2337* (all MO). Río Maestro, *Gentry 2212, 2215* (both MO). Near Río Partí, *Gentry 3800* (MO). Río Bayano above Río Espavé, *Gentry 3850* (MO). San José Island, *Johnston 508* (GH), *1161* (BM, GH, MO, P, U, US). Agricultural Experiment Station at Matías Hernández, *Pittier 6861* (BM, F, GH, MO, NY, US). SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1502* (MO). VERAGUAS: Above Santa Fé, *Gentry 3024* (MO).

6. CERATOPHYTUM

Ceratophytum Pittier, Jour. Washington Acad. Sci. 18: 62. 1928. TYPE: *C. capricorne* Pittier = *C. tetragonolobum* (Jacq.) Sprague & Sandw.

Lianas; stems with 4 phloem arms in cross section; branchlets terete, with conspicuous interpetiolar glandular fields; pseudostipules of 3 acute, more or less subulate scales appressed against the twig. *Leaves* 3-foliolate, the terminal leaflet often replaced by a trifid tendril. *Inflorescence* a few-flowered terminal, subcorymbose panicle. *Flowers* with the calyx cupular, more or less truncate, coriaceous, lepidote, with short, linear, glandular fields descending from the rim; corolla cream to pale yellow, thick, tubular-campanulate, pubescent outside; anthers glabrous, the thecae straight, divaricate; pollen grains simple, 3-colporate, the exine reticulate; ovary narrowly cylindric, more or less lepidote, the ovules 6–8-seriate in each locule; disc pulvinate-cupular. *Fruit* an oblong-linear, subtetragonal capsule; gibbous at the base and tapering to the apex, the valves parallel to the septum, not flattened, smooth; seeds bialate, the wings papery, brownish, the tip usually subhyaline, not clearly demarcated from the seed body.

One species ranging from Mexico to Trinidad and Guyana.

Ceratophytum tetragonolobum (Jacq.) Sprague & Sandw., Kew Bull. 1934: 222. 1935.—FIG. 6.

Bignonia tetragonoloba Jacq., Fragm. Bot. 36, *tab. 40, fig. 2.* 1800–1809. TYPE: Venezuela, Caracas (not seen).
Anemopaegma tobagense Urb., Fedde Repert. 14: 311. 1916. TYPE: Tobago, *Broadway 3493* (K, NY).
Ceratophytum capricorne Pittier, Jour. Washington Acad. Sci. 18: 63. 1928. TYPE: Venezuela, Distrito Federal, *Pittier 11527* (K, US, VEN).
C. brachycarpum Pittier, Jour. Washington Acad. Sci. 18: 65. 1928. TYPE: Venezuela, Aragua, *Pittier 11805* (K, fragments; US, VEN).
Adenocalymma heterophyllum Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 49. 1930, non Kränzl. TYPE: Mexico, Yucatan, *Gaumer & Sons 23889* (F).
Ceratophytum tobagense (Urb.) Sprague & Sandw., Kew Bull. 1933: 322. 1933.
Adenocalymma standleyanum Lundell, Carnegie Inst. Washington Publ. 478: 221. 1937. TYPE: Based on *A. heterophyllum* Standl.

Liana to at least 7 cm in diameter, stem often indistinctly 4-parted and twisted, the nodes with a swollen annulus, the bark gray, smooth, sometimes with raised whitish lenticels; stem with 4 phloem arms in cross section; branchlets terete, longitudinally finely striate, lepidote, the nodes with interpetiolar glandular fields; pseudostipules of 3 subulate scales, appressed against the twig

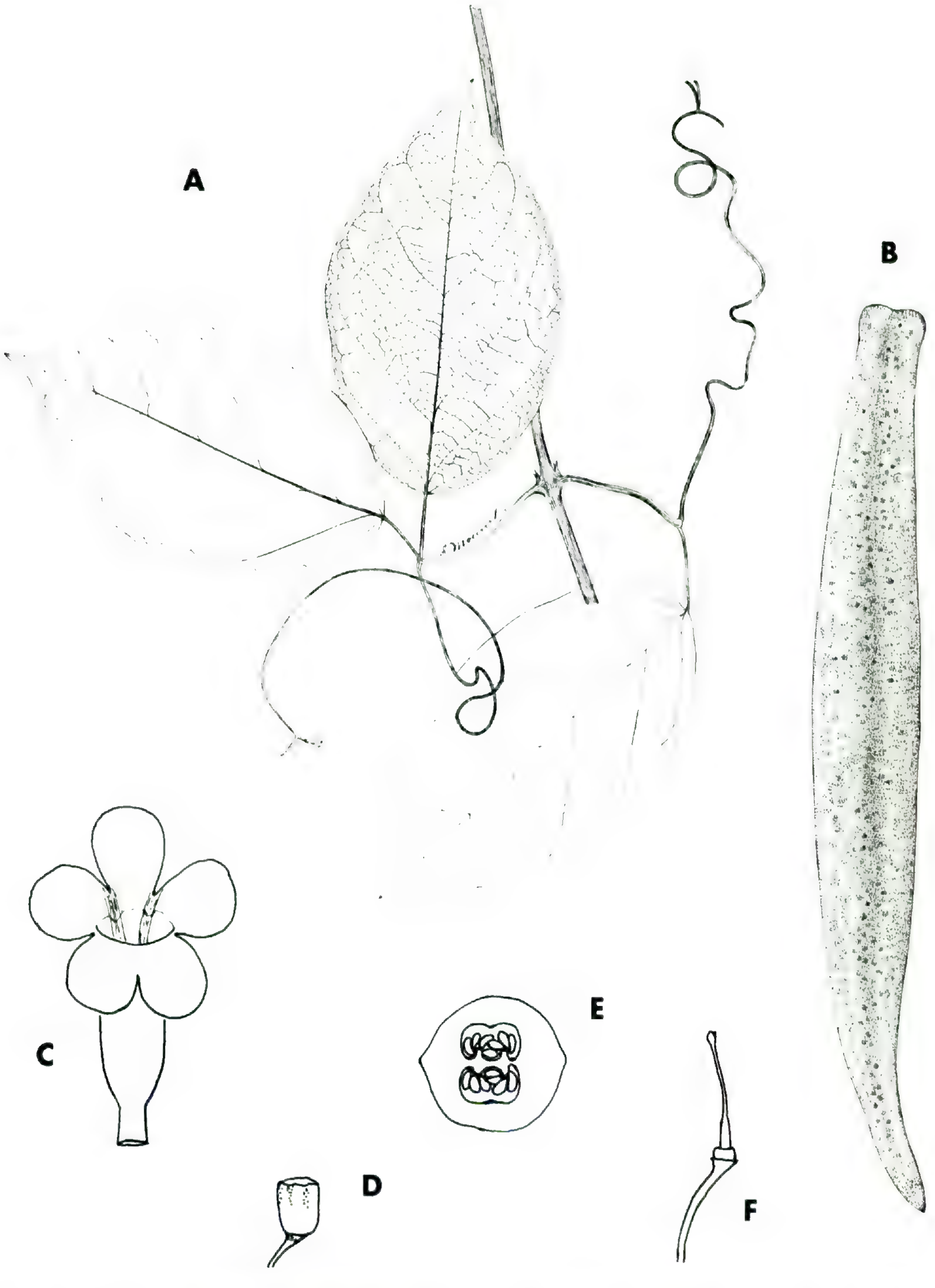

FIGURE 6. *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw.—A. Habit (× ⅜). [After *Gentry 722* (MO).]—B. Fruit (× ⅜). [After *Gentry 3838* (MO).]—C. Corolla (× ½).—D. Calyx (× ½).—E. Ovary cross section (× 9).—F. Pistil and disc (× ½). [After *Gentry 2195* (MO).]

when fresh, when dry the 2 outer scales divergent. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets oblong-ovate to elliptic-obovate, acute to obtuse, truncate to asymmetrically subcordate, 6.2–18 cm long and 2.1–15 cm wide, membranaceous to chartaceous, secondary veins 5–6 on a side, mostly glabrous or inconspicuously lepidote, inconspicuously simple-puberulent in the nerve axils beneath and at the base of the main veins above, drying olive; tendril trifid, 5–20 cm long to branching, the 3 arms 0.4–2.5 cm long; terminal petiolule 2.1–4.6 cm long, laterial petiolules 0.3–5.7 cm long; petiole 3.0–12 cm long, lepidote or sparsely puberulous as the petiolules. *Inflorescence* a terminal, few-flowered, subcorymbose panicle, often contracted to one or 2 flowers, its branches lepidote. *Flowers* with the calyx cupular, truncate, 8–13 mm long and 9–10 mm wide, lepidote, with 4–6 linear glandular fields descending from the rim; corolla thick, cream-colored to pale yellow outside and on the lobes inside, the throat yellow inside; tubular-campanulate, 7.7–8.1 cm long and 1.7–2.1 cm wide at the mouth, the tube 5.6–5.8 cm long, glabrous inside but densely pubescent with long, simple, multicellular hairs just below the level of stamen insertion, the lobes 1.6–2.2 cm long, densely glandular-lepidote to glandular-pubescent outside, glandular-lepidote on the lobes; stamens didynamous, the anther thecae divaricate, 4.5–6 mm long, the longer filaments 2.2–2.4 cm long, the shorter filaments 1.4–1.6 cm long, the staminode 5–6 mm long, inserted 9–12 mm from the base of the corolla tube; pistil 3.2–3.3 cm long, the ovary narrowly cylindric, 5 mm long, 2 mm wide, lepidote, the ovules 6–8 seriate in each locule; disc pulvinate-cupular, 2 mm long, 4 mm wide. *Capsule* cylindrical, basally gibbous, tapering upwards, 26–39 cm long and 3–3.9 cm wide, 2.2–2.6 cm thick, the surface tan, more or less lepidote; seeds biseriate, 0.8–1.8 cm long and 3.4–6.3 cm wide, the wings papery, brown, not demarcated from the seed body.

A vine characteristic of the tropical moist forest, it is seldom common and is poorly represented in herbaria, despite its wide range from Mexico to Surinam. It has been collected in flower in Panama in April (Barro Colorado Island and Madden Lake) and late October (Rio Pasiga), in each instance two widely separated individuals blooming on the same day.

The presence of *Paragonia*-like pseudostipules with interpetiolar glandular fields serves to distinguish sterile specimens of *C. tetragonolobum*. Trifid tendrils are another good field mark.

A fallen fruit collected from a stream bed at Almirante, Bocas del Toro Province, may belong to *Ceratophytum*. It is of the characteristic shape but much narrower and only 13 cm long. It could belong to a new species of this genus.

CANAL ZONE: Barro Colorado Island, *Croat 10212, 10808, 10879* (all MO), *14453, 14458* (both MO, SCZ), *14865* (SCZ), *14925* (MO). Boy Scout road near Madden Lake, *Gentry 2054* (MO). Margarita, *Gentry & Tyson 4831* (MO). Fort Sherman, *Gentry & Tyson 4838* (MO). DARIÉN: S of La Palma, *Gentry 4292* (MO). Río Tuira between Ríos Paya and Espavé, *Gentry 4398* (MO). Between Ríos Cube and Punusa, *Gentry 4453* (MO). El Real, *Gentry 4537* (MO). Río Parasenico near Cerro Pirre, *Gentry 4739* (MO). PANAMÁ: Between El Llano and Río Mamoní, *Duke 5368* (GH, MO). Between Cañitas and Bayano dam site, *Gentry & Tyson 1705* (MO). Río Pasiga, *Gentry 2195, 2273, 2320* (all MO). Near Icantí, *Gentry 2601* (MO). Near Río Espavé, *Gentry 3699* (MO). S of Río Bayano, in Cuna reserva-

tion, *Gentry 3814*, 3838 (both MO). SAN BLAS: Near Puerto Obaldía, *Gentry 1525*, *1569* (both MO).

7. CLYTOSTOMA

Clytostoma Miers *ex* Bur., Adansonia 8: 353. 1868. TYPE: *C. callistegioides* (Cham.) Bur. *ex* Griseb.

Lianas, stems with 8 phloem arms in cross section; branchlets tetragonal to subterete without interpetiolar glandular fields; pseudostipules variable, usually a cluster of subulate-lanceolate cataphylls more or less resembling a minute bromeliad. *Leaves* simple to 2-foliolate, often with a terminal simple tendril. *Inflorescence* a few-flowered panicle or a one to few-flowered axillary or terminal fascicle. *Flowers* with the calyx cupular to campanulate, truncate, usually more or less 5-denticulate, variously sublepidote to subpuberulous; corolla white to purple, tubular-infundibuliform, somewhat puberulous or glandular lepidote outside; anthers glabrous, the thecae straight, divaricate; pollen grains ecolpate, the exine finely reticulate; ovary ovoid-cylindric, minutely blunt-tuberculate with thick one-celled glandular trichomes, the ovules 2(–4)-seriate in each locule. *Fruit* an ellipsoid or suborbicular capsule, the valves parallel to the septum, woody, echinate with retrorse spines; seeds thick, corky, essentially wingless.

Nine species in continental tropical America ranging from Mexico to Uruguay, Argentina and Brazil.

1. **Clytostoma binatum** (Thunb.) Sandw., Recueil Trav. Bot. Neerl. 34: 235. 1937.—FIG. 7.

Bignonia binata Thunb., Pl. Bras. 3: 35. 1821. TYPE: Brazil, *Freyreiss s.n.* (UPS, fide Sandw.).
B. callistegioides forma β Cham., Linnaea 7: 714. 1832. TYPE: Brazil, *Sellow* s.n. (NY).
B. noterophila Mart. *ex* DC., Prodr. 9: 148. 1845. TYPE: Brazil, Para, *Martius s.n.*, 1819. (M).
B. umbellata DC., Prodr. 9: 148. 1845. TYPE: Brazil, *Lhotsky s.n.* (G-DC.).
B. purpurea Lodd. *ex* Hook. f., Bot. Mag. *tab.* 5800. 1769. TYPE: (not seen).
Adenocalymma ocositense Donn. Sm., Bot. Gaz. (Crawfordsville) 18: 209. 1893. TYPE: Guatemala, Quetzaltenango, *J. D. Smith 2688* (GH, K, M, NY, US).
Clytostoma floridum Miers *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 154. 1896, pro syn.
C. noterophilum (Mart. *ex* DC.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 153. 1896.
C. purpureum (Lodd. *ex* Hook. f.) Rehder *in* Bailey, Standard Cycl. Hort, 2: 806 1914.
C. isthmicum Pittier, Contr. U.S. Natl. Herb. 18: 257, *pl. 106*. TYPE: Panama, Canal Zone, *Pittier 4008* (BM, GH, NY, US).
Petastoma laurifolium Kränzl., Fedde Repert. 17: 57. 1921. TYPE: Bolivia, junction of Ríos Beni and Madre de Dios, *Rusby 1144*, pro parte (B, K, MICH).
P. multiglandulosum Kränzl., Fedde Repert. 17: 58. 1921. TYPE: Bolivia, junction of Ríos Beni and Madre de Dios, *Rusby 1145* (K).
P. ocositense (Donn. Sm.) Kränzl., Fedde Repert. 17: 61. 1935.

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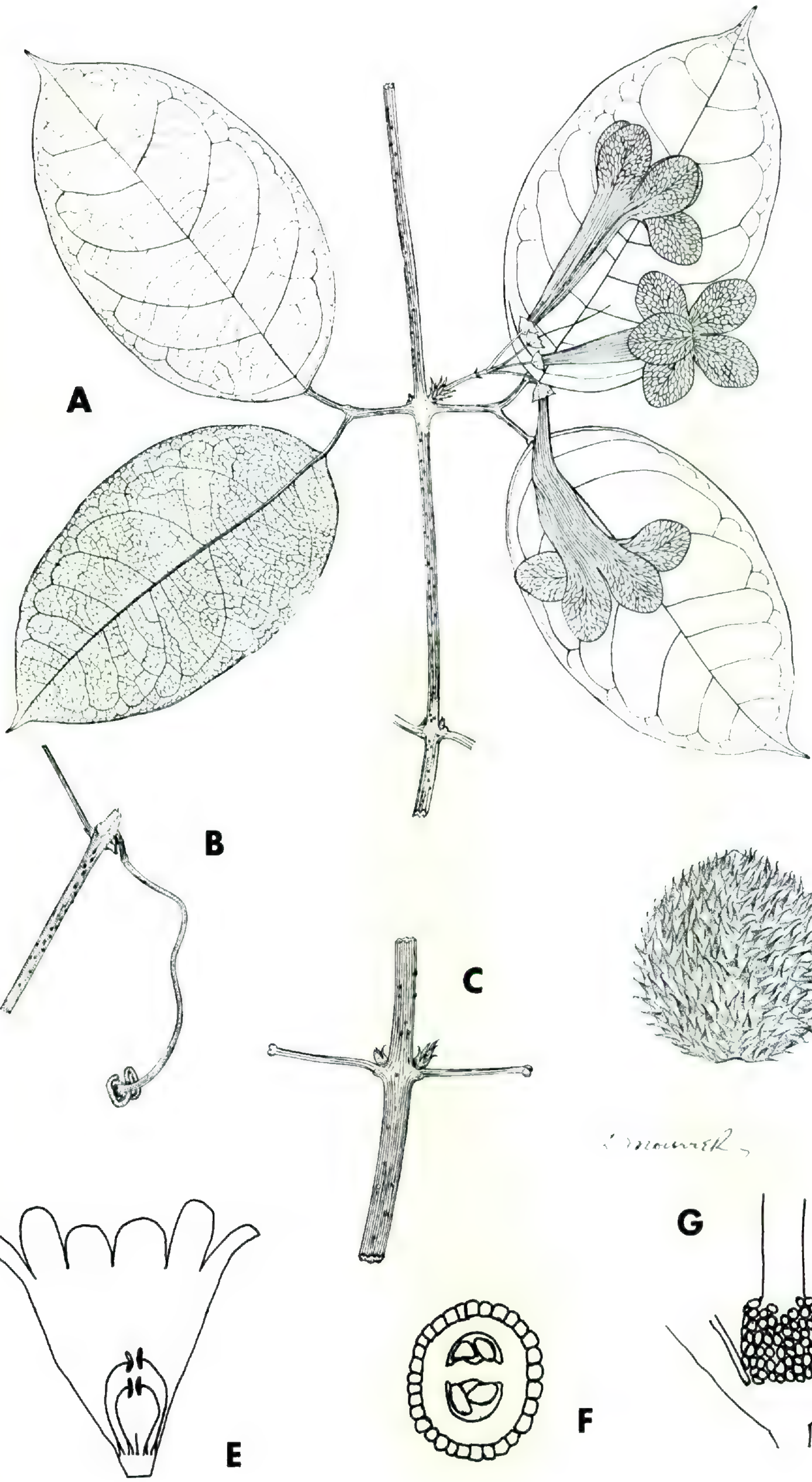
FIGURE 7. *Clytostoma binatum* (Thunb.) Sandw.—A. Habit (× ½). [After *Gentry 3781* (MO).]—B. Tendril (× ⅗). [After *Gentry 5127* (MO).]—C. Node with pseudostipules (× ⅗). [After *von Wedel 788* (MO).]—D. Fruit (× ⅗). [After *Gentry 3756* (MO).]—E. Corolla split open (× ⅗).—F. Ovary cross section (× 12).—G. Ovary (× 7). [After *Gentry 3740* (MO).]


A
B
C
D
E
F
G

Clytostoma elegans Standl., Carnegie Inst. Washington Publ. 461: 86. 1935. TYPE: British Honduras, Río Grande, *Schipp 1127* (F, holotype; K, MO, US, isotypes).
C. ocositense (Donn. Sm.) Seib., Carnegie Inst. Washington Publ. 522: 413. 1940.

Liana to at least 5 cm in diameter, the bark gray, smooth; stem with 8 phloem arms in cross section; branchlets subtetragonal, lepidote and slightly puberulous, the nodes without interpetiolar glandular fields, pseudostipules usually resembling small bromeliads, composed of numerous small acute bracts. *Leaves* 2-foliolate, sometimes with a tendril; leaflets elliptic, acuminate, basally cuneate, 6.5–19 cm long and 2.4–7.9 cm wide, membranaceous to chartaceous, secondary veins 5–9 on each side, plate-shaped glands along midvein especially near base, lepidote on both sides, otherwise glabrous beneath, minutely puberulous at the base of the midvein above, drying greenish above, olive beneath; tendril simple, 5–12 cm long; petiole and petiolules minutely puberulous on upper surface, petiolules 0.5–2.1 cm long, slightly swollen and woody at base and apex, petiole 0.6–3.1 cm long. *Inflorescence* an axillary or terminal fascicle, the pedicels scabrous. *Flowers* aromatic, calyx cupular, subtruncate or 5-denticulate with cusps to 1 mm long, 4–7 mm wide, subpuberulous to scabrous, usually with plate-shaped glands in the upper half; corolla magenta to almost white outside and on the lobes inside, the throat white inside with ca. 11 thin longitudinal magenta nectar guide lines on the abaxial side, usually with a deeper magenta spot at the base of the adaxial sinus, tubular-infundibuliform, 5–8.5 cm long and 1.2–2.4 cm wide at the mouth, the tube 3.7–5.8 cm long, the lobes 1.2–2.2 cm long, puberulous outside with simple or sometimes branched trichomes and slightly glandular-lepidote on the lobes, inside more or less glandular-lepidote on the lobes, mostly glabrous in the tube with plate-shaped glands scattered adaxially, glandular-pubescent with simple trichomes at and below the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2–3 mm long, the longer filaments 1.4–1.9 cm long, the shorter filaments 1.0–1.3 cm long, the staminode 3–5 mm long, inserted 4–6 mm from base of corolla tube; pistil 2.4–2.7 cm long, the ovary rounded short-cylindric, 2 cm long and 1.5–2 cm wide, 1–1.5 cm thick, densely covered with thick subspherical glandular trichomes, the ovules 2-seriate in each locule; disc obsolete. *Capsule* elliptic to suborbicular, heavily echinate with the tips of the enations recurved and often split, 4.5–6.5 cm long and 3.2–4.5 cm wide; seeds thick, corky, 1.2–1.9 cm long and 1.9–2.4 cm wide, the wings brown, woody, almost obsolete.

Ecologically restricted mainly to swampy or lakeshore habitats in the tropical wet forest, this species occurs less commonly in moister parts of the tropical moist forest, *e.g.* a single plant known on Barro Colorado Island. Its swampy habitat precludes abundant herbarium representation despite its relatively high local abundance. It ranges from Mexico to Brazil. This species flowers sporadically throughout the year but is most commonly collected in late wet season (September to November). The seeds are water dispersed as befits its swamp habitat.

Clytostoma binatum resembles *Cydista aequinoctialis* when sterile and is best separated by its bromeliad-like pseudostipules, which are unfortunately

often absent. The 4 darker lines on a subterete to subtetragonal twig are characteristic as is the elliptic leaf shape.

BOCAS DEL TORO: Region of Almirante, *Cooper 198* (F). Banks of Changuinola River near Bar Mouth, *Dunlap 418* (BM, F, GH, US). 10–15 mi. inland from mouth of Changuinola River, *Lewis et al. 866*. Vicinity of Chiriqui Lagoon, *von Wedel 9, 788* (both GH, MO), *1314* (US), *1345* (GH, MO). Water Valley, *von Wedel 795* (GH, MO, US), *1660* (MO). Fish Creek Mountains, *von Wedel 2360* (GH, MO, US). Western River, *von Wedel 2700* (MO). CANAL ZONE: Barro Colorado Island, *Croat 5727* (MO), *13963* (MO, SCZ). S of Margarita, *Gentry 5127* (MO). Bohio Station of Panama Railroad, *Hayes 144* (K). Panama Station, Panama Railroad, *Hayes 412* (BM). Along Río Trinidad, *Pittier 4008* (BM, GH, NY, US). COLÓN: E of Río Piedras, *Gentry 2190* (MO). Peluca Hydrographic Station, *Steyermark & Allen 17224* (BM, K, MO). DARIÉN: El Real, *Duke 5055* (GH, MO, PMA, US); *Gentry 4572* (MO). Near Pinogana, *Pittier 6526* (US). PANAMÁ: Río Espavé, *Gentry 3740, 3756, 3781* (all MO). Between Juan Mina and Vigía, *Pittier 3452* (BM, NY, US).

8. CRESCENTIA

Crescentia L., Sp. Pl. 2: 626. 1753; Gen. Pl., ed. 5. 274. 1754. TYPE: *C. cujete* L.

Pteromischus Pichón, Bull. Soc. Bot. France 92: 227. 1946. TYPE: *P. alatus* (H.B.K.) Pichón
= *Crescentia alata* H.B.K.

Small to medium-sized *trees*, branching rachitic, crown open. *Leaves* simple or 3-foliolate, borne on thick twigs in alternate fascicles resulting from the condensation of short-shoots. *Inflorescence* of 1-2 cauliflorous flowers arising from nodes on the trunk and older branches. *Flowers* with the calyx large, usually bilabiately split; corolla off-white, usually with maroon penciling, especially on lobes and on the tube inside, the lobes deltoid, acuminate; stamens subexserted, the anthers glabrous, the thecae thick, somewhat divergent; pollen grains single, 3-colpate, the exine microreticulate; ovary ovoid-elliptic, lepidote, 1-locular, the ovules multi-seriate on 4 parietal placentae. *Fruit* a pepo or calabash, large, more or less spherical, indehiscent with a hard woody shell, pulpy inside; seeds small, less than 8 mm long and 9 mm wide, flat, not winged, embedded in the pulp.

Five species in tropical America ranging from Mexico and the West Indies to Amazonian Brazil, also cultivated through most of the tropics. Probably not native to Panama.

a. Leaves all simple, more than 3.4 cm long; fruit more than 13 cm in diameter, widely cultivated ..... 2. *C. cujete*
aa. Leaves 3-foliolate and simple in each fascicle, the simple leaves less than 3.2 cm long; fruit less than 10 cm in diameter, rarely cultivated ..... 1. *C. alata*

1. **Crescentia alata** H.B.K., Nov. Gen. Sp. Pl. 3: 158. 1819. TYPE: Mexico, Guerrero, *Humboldt & Bonpland 3858* (P).—FIG. 8F–G.

C. trifolia Blanco, Fl. Filip., ed. 1. 489. 1837. TYPE: (not seen).
Parmentiera alata (H.B.K.) Miers, Trans. Linn. Soc. 26: 166. 1868.
Crescentia ternata Sessé & Moc., La Naturaleza, ser. 2. 1 (append.): 94. 1889. TYPE: Mexico (not seen; photo of illustration at MO).
Pteromischus alatus (H.B.K.) Pichón, Bull. Soc. Bot. France 92: 227. 1945.

Small *tree* to 25 cm d.b.h. and 6 m tall, the branches crooked, the crown open; branchlets essentially lacking, the smaller branches thick, subterete, with

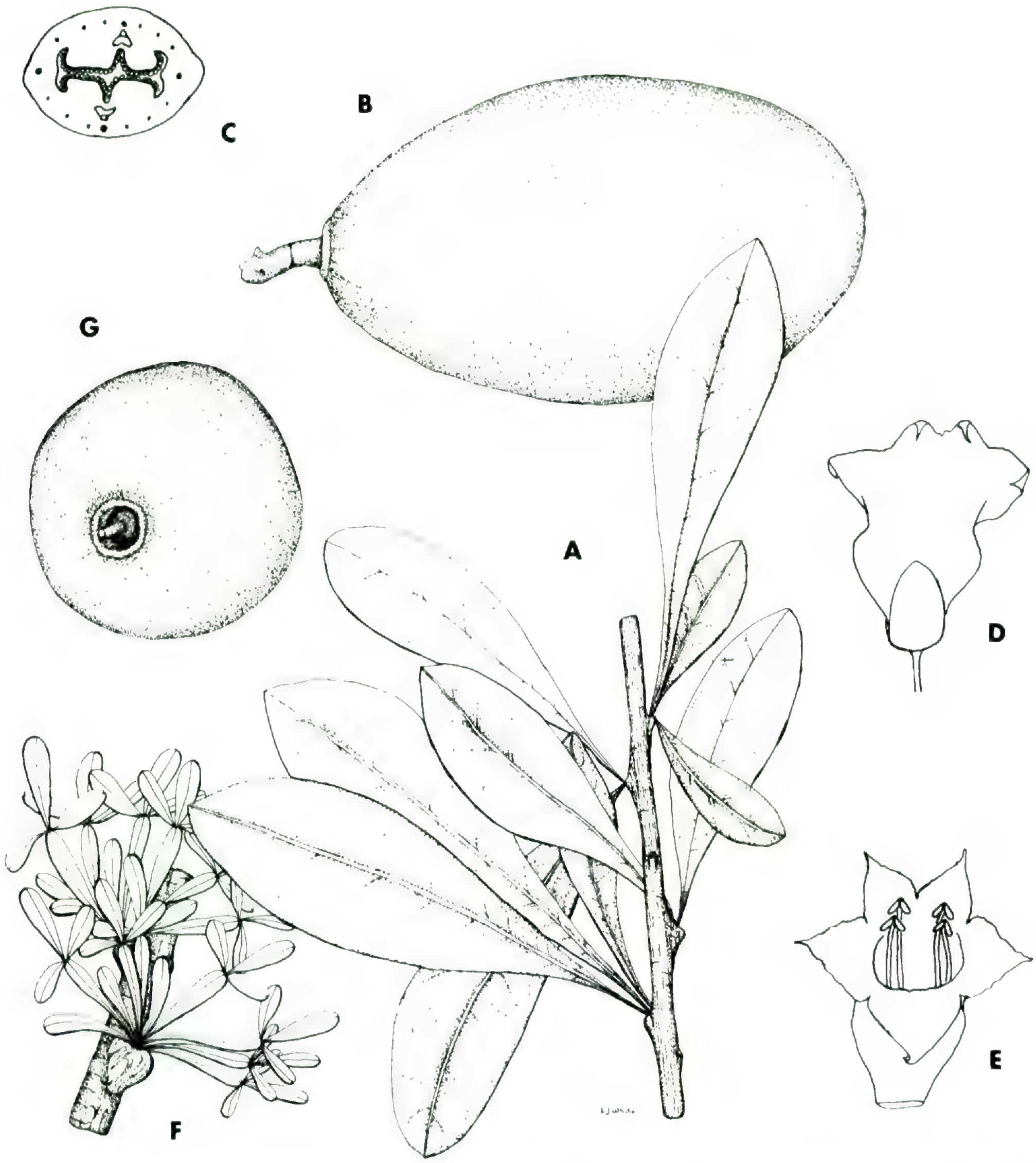


Figure 8. *Crescentia*.—A–E. *C. cujete* L.—A. Habit (× 2/5).—B. Fruit (× 2/5). [After *Gentry* 352, Costa Rica (MO).]—C. Ovary cross section (× 4).—D. Flower in dorsal view (× 2/5).—E. Corolla in ventral view (× 2/5). [From miscellaneous fresh material.]—F–G. *C. alata* H.B.K.—F. Habit (× 2/5). [After *Croat* 273, Costa Rica (MO).]—G. Fruit (× 2/5). [After *Gentry* 5043, Mexico (MO).]

alternate condensed, short-shoot projections each bearing a fascicle of leaves from its center. *Leaves* both compound and simple from each fascicle, the compound leaves 3-foliolate with sessile oblanceolate leaflets 1.0–4.5 cm long and 0.3–1.2 cm wide, round-tipped or slightly emarginate, lepidote but otherwise glabrous, rigid-chartaceous, the petiole winged, 2.7–11.5 cm long and 3–15 mm wide, lepidote, oblanceolate, rigid chartaceous as the leaflets, the simple leaves much smaller, 1.9–3.2 cm long and 0.5–1.0 cm wide, similar to single leaflets or

petioles of compound leaves. *Inflorescence* one or 2 cauliflorous flowers borne on larger branches or trunk, pedicels lepidote, 0.5–0.8 cm long. *Flowers* with a musky odor, calyx split nearly to the base into two subequal lobes, each 1.4–1.9 cm long and 0.7–1.4 cm wide, mostly glabrous, slightly lepidote at the base, usually with sunken plate-shaped glands; corolla off-white, tubular-campanulate with a horizontal pleat midway across the lower side of throat, fleshy, 4.0–6.5 cm long and 1.8–2.5 cm wide at the mouth of tube, the tube 2.8–4.2 cm long, the lobes 1–1.5 cm long, more or less triangular and fused at the bases, mostly glabrous, sparsely glandular-lepidote outside; stamens subexserted, the anther thecae ca. 2 mm thick, only partially divergent, 5–7 mm long, the anterior filaments 2.1–3.4 cm long, inserted 0.8–1.7 cm from the base of the tube, the posterior filaments 2.3–3.8 cm long, inserted 1.1–1.5 cm from the base of tube, the staminode 3–4 mm long, inserted 0.9–1.0 cm from the base of the tube; pistil 4.3–5.8 cm long, the ovary rounded-conical, lepidote, 5–6 mm long and 4–5 mm wide, the ovules multi-seriate on 4 parietal placentae; disc pulvinate, 2–3 mm long and 0.9–1.4 mm wide. *Fruit* a pepo or calabash, more or less spherical, 7–10 cm in diameter; seeds small, thin, wingless, 6–7 mm long and 7–9 mm wide, scattered through the pulp of the fruit.

A plant of the tropical dry forest from Mexico to Guanacaste, Costa Rica, *C. alata* is much confused with its better known congener *C. cujete*. It is actually the commoner of the two in the wild and is in fact a characteristic tree of Pacific slope dry forest savannas, its short twisted stature and open rachitic branching making it physiognomically one of the most conspicuous elements of this vegetation. It flowers irregularly throughout the year. The fruit is similar to that of *C. cujete* but smaller. Presumably the fruit is water dispersed and the seeds dispersed by large mammals. I have encountered young trees of this species growing far from the usual savanna habitat on gravel bars where they must have grown from water-carried fruits.

Apparently this tree is neither utilized nor cultivated by the campesinos, who prefer its larger-fruited relative; there are reports, however, of the fruits being used as cups. The 3 leaflets and petiole together form a kind of cross and the tree has acquired some religious significance from this resemblance.

The 3-foliolate leaf of this species is the best mark distinguishing it from the simple-leaved *C. cujete*. Smaller fruit size is also a useful character. The two species hybridize and two much-studied trees along the Pan-American Highway at Hacienda la Pacifica near Cañas, Costa Rica, are apparent hybrids. These trees have the small fruits of *C. alata* but the simple leaves of *C. cujete*, and occasional branches bear 3-foliolate leaves. Trees of both putative parent species occur in the immediate vicinity.

CHIRIQUÍ (VERAGUAS): Davíd, cultivated *Seemann 1130* (K).

2. **Crescentia cujete** L., Sp. Pl., ed. 1. 2: 626. 1753. TYPE: Specimen without information (LINN 779.1).—FIG. 8A–E.

C. acuminata H.B.K., Nov. Gen. Sp. Pl. 3: 157. 1819. TYPE: Cuba, Havana, *Humboldt & Bonpland 1300* (P).
C. arborea Raf., Sylva Tell. 81. 1838. TYPE: (not seen).

C. cuneifolia Gardn., Jour. Bot. (Hook.) 2: 422. 1840. TYPE: Brazil, Goyaz, *Gardner 3342* (K).
C. angustifolia Willd. *ex* Seem., Trans. Linn. Soc., ser. 1. 23: 20, 1862, pro syn.
C. fasciculata Miers, Trans. Linn. Soc., ser. 1. 26: 171. 1868. TYPE: St. Thomas, *Oersted s.n.* (not seen).
C. plectantha Miers, Trans. Linn. Soc., ser. 1. 26: 170. 1868. TYPE: Brazil, Rio de Janeiro (not seen).
C. spathulata Miers, Trans. Linn. Soc., ser. 1. 26: 173. 1868. TYPE: Ecuador, *Sinclair s.n.* (K).
C. cujete var. *puberula* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 403. 1897. SYNTYPES: Brazil, Goyaz, *Dombey s.n.* (not seen); Peru, *Ruiz s.n.* (not seen).

Tree to 10 m tall and 30 cm d.b.h., the branches usually crooked, the crown open; branchlets mostly lacking, smaller branches thick, subterete, with alternate short-shoot projections each bearing a fascicle of leaves from its center. *Leaves* of various sizes within each fascicle, simple, obovate, the tip obtuse to acute, the base attenuate, petiole lacking, 3.4–26 cm long and 1.0–7.6 cm wide, chartaceous to rigid-chartaceous, secondary veins 5–14 on a side, the midvein raised above; lepidote above and beneath, otherwise glabrous above, beneath pubescent along midvein with simple and forked trichomes, plate-shaped glands at base of blade beneath, drying grayish-olive. *Inflorescence* one or 2 cauliflorous flowers borne on larger branches or trunk, the pedicels lepidote, 1.5 cm long. *Flowers* with a musty odor, calyx bilabiately split to the base, each lobe 1.8–2.6 cm long and 1.3–2.4 cm wide, mostly glabrous with plate-shaped glands on the upper half of lobes, slightly lepidote at the base; corolla off-white to yellowish-white with purplish venation on the lobes and purplish lines on the tube outside, tubular with a transverse fold midway across the lower side of the throat, fleshy, 4.1–7.4 cm long and 3.1–4.5 cm wide at the mouth of the tube, the tube 2.8–4.5 cm long, the lobes triangular with the apex extended as a narrow point, 2.5–3.1 cm long, sparsely lepidote or stalked-lepidote on the tube outside and near the mouth of tube inside, more densely so at the level of stamen insertion, papillate-glandular on the lobes outside and sparsely so inside; stamens subexserted, the anther thecae thick, partially divergent, 5–8 mm long and 2.5–3.5 mm wide, the anterior filaments 2.8–3.2 cm long and inserted 6–11 mm from the base of the tube, the posterior filaments 2.8–3.3 cm long, inserted 7–15 mm from the base of the tube, the staminode 1–3 mm long, inserted 5–11 mm from the base of the tube; pistil 4.0–4.9 cm long, the ovary rounded conical, 5–7 mm long and 4–7 mm wide, 3–6 mm thick, lepidote, the ovules multi-seriate on 4 placentae; disc annular-pulvinate, 3–4 mm long and 8–11 mm wide. *Fruit* a pepo or calabash, spherical to ovoid-elliptic, 13–20 cm in diameter to 30 cm long, the thin hard shell smooth, lepidote-punctate; seeds small, thin, wingless, 7–8 mm long and 4–6 mm wide, scattered through the pulp of the fruit.

Crescentia cujete is extensively cultivated through most of tropical America. Although native to Central America, such wide cultivation makes its original range impossible to trace. Apparently wild-growing trees are sometimes encountered, but even these may have descended from cultivated trees. It flowers irregularly throughout the year. The flowers are bat-pollinated. The fruit floats and can sometimes be found washed up on beaches indicating a possible means of dispersal.

The hard shell of the fruit is widely used as a utensil for dipping or holding

liquids. They are especially conspicuous as bailers for piraguas, and nearly every piragua in Panama's Darién is equipped with its piece of *Crescentia* exocarp. The pulp is edible but insipid-tasting and little used for food.

BOCAS DEL TORO: Near Almirante, *Gentry 2807* (MO). Mariano Creek, *von Wedel 2894* (GH, MO). CANAL ZONE: Near Los Ríos, *Gentry 3690* (MO). Gatun Station, *Hayes 94* (BM). Balboa Heights, *Sharp s.n.* (SCZ). Chiva Chiva Trail, *Tyson & Blum 3565* (SCZ). CHIRIQUÍ: Without locality, *Wagoner s.n.* (M). Progreso, *Cooper & Slater 288* (US). DARIÉN: Village of Paya, *Gentry 4397* (MO). El Real, *Gentry 4505* (MO). LOS SANTOS: S of Pedasí, *Stimson 5293* (MO, SCZ). PANAMÁ: Cañitas, *Gentry 1405* (MO). Río Maestro, *Gentry 2245* (MO). Río Piragua (Tabardí), *Gentry 2523* (MO). Bella Vista, *Standley 25343* (US). Taboga Island, *Standley 27885* (US). Between Matías Hernándes and Juan Díaz, *Standley 31974* (US). SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1478* (MO).

9. CUSPIDARIA

Cuspidaria DC., Rev. Bign. (Bibl. Univ. Genève) 8. 1838, nom. cons. TYPE: *B. pterocarpa* Cham. = *Cuspidaria pterocarpa* (Cham.) DC.

Lochmocydia Mart. *ex* DC., Prodr. 9: 177. 1845, pro syn.
Saldanhaea Bur., Adansonia 8: 354. 1868, non *Saldanha* Vell., 1825. TYPE: *S. lateriflora* (DC.) Bur.
Blepharitheca Pichón, Bull. Soc. Bot. France 92: 224. 1945. TYPE: *B. floribunda* (DC.) Pichón = *Cuspidaria floribunda* (DC.) A. Gentry.

Lianas, branchlets terete, with or without interpetiolar glandular fields; pseudostipules small or lacking. *Leaves* simple to 5-foliolate, sometimes with a simple tendril. *Inflorescence* a terminal panicle, often on a short lateral branch. *Flowers* with the calyx cupular, 5-denticulate, the teeth usually long and conspicuous; corolla lavender, tubular-infundibuliform, puberulous outside; anthers pubescent or glabrous, the thecae divaricate, bent at the middle and strongly reflexed forward; pollen grains in tetrads; ovary linear-cylindric, lepidote, the ovules 2–4-seriate in each locule. *Fruit* a linear or oblong capsule, the valves more or less woody though sometimes quite thin, parallel to the septum, with conspicuously raised more or less winged lateral margins or with 2 submarginal ridges, in either case with a more or less evident central furrow on each valve; seeds thin, bialate, the wings hyaline-membranaceous.

About 10 species in continental tropical America from eastern Panama to Argentina, mostly in Brazil.

Cuspidaria floribunda (DC.) A. Gentry, Brittonia 25: 232. 1973.—FIG. 9.

Adenocalymma floribundum DC., Prodr. 9: 201. 1845, non *Bignonia floribunda* H.B.K., *Arrabidaea floribunda* (H.B.K.) Loes. TYPE: Bolivia, Santa Cruz, *d'Orbigny 533* (P).
Arrabidaea rubrinervis Miers, Proc. Roy. Hort. Soc. 3: 192. 1863. TYPE: Brazil, São Paulo, *Wier 178* (BM, K).
A. subfastigiata Bur. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 70. 1896. TYPE: Brazil, Minas Gerais, *Warming s.n.* (BR).
A. macrocarpa O. Kuntze, Rev. Gen. Pl. 3(2): 242. 1898. TYPE: Bolivia, Velasco, *Kuntze s.n.* (NY).
Blepharitheca floribunda (DC.) Pichón, Bull. Soc. Bot. France 92: 224. 1945.
Saldanhaea subfastigiata (Bur.) J. C. Gomes, Rev. Bras. Biol. 9: 51. 1951.
S. floribunda (DC.) Sandw., Kew Bull. 22: 408. 1968.

Liana without interpetiolar glandular fields or noticeable pseudostipules;

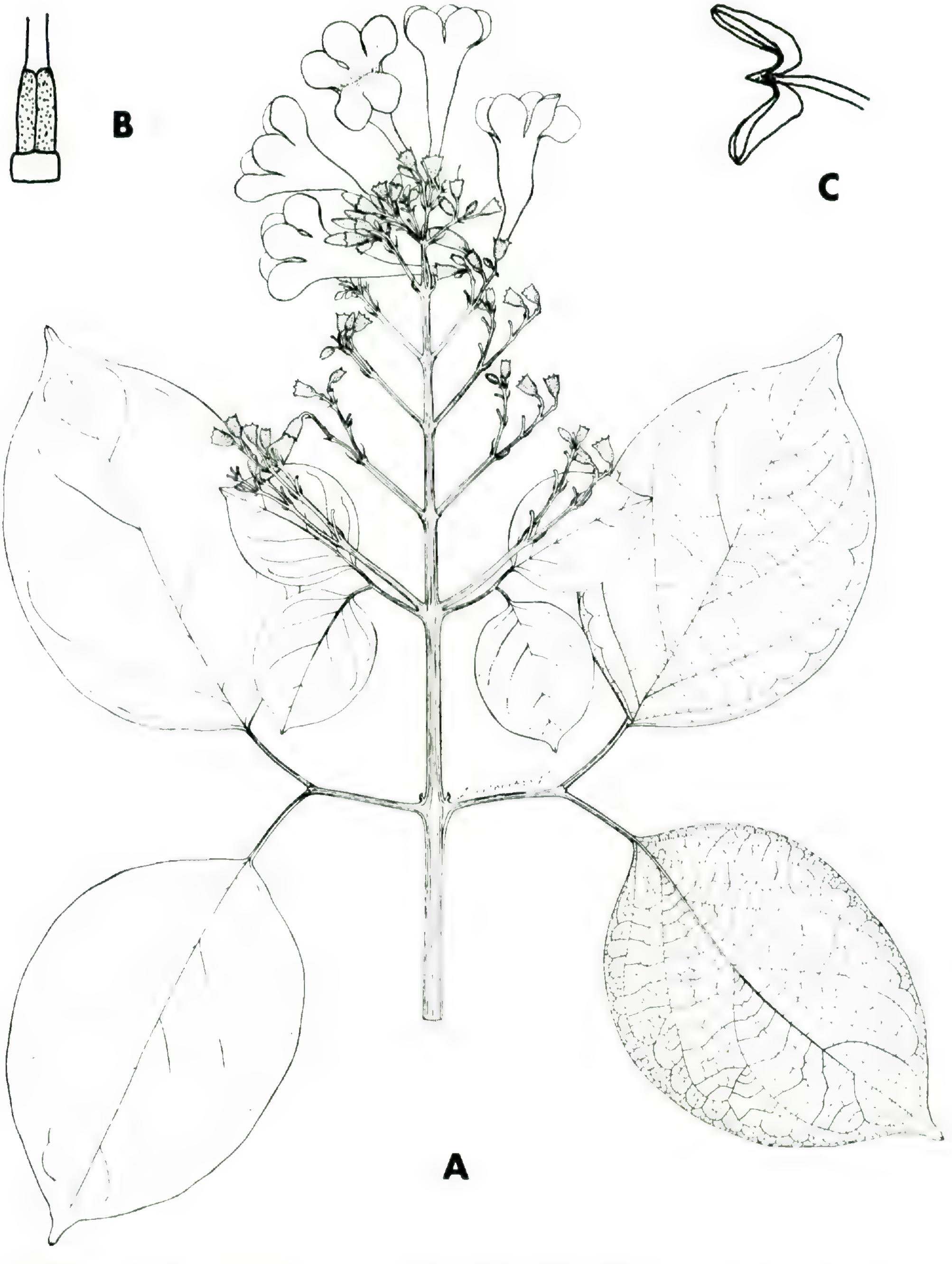


FIGURE 9. *Cuspidaria floribunda* (DC.) A. Gentry.—A. Habit (× ½).—B. Ovary and disc (× 6).—C. Anther (× 6). [After *Duke* 5386 (MO).]

branchlets subterete, flattened at nodes, sometimes with conspicuous V-shaped interpetiolar ridges, longitudinally striate when dried, noticeably lenticellate, appressed puberulous, sometimes hollow at the very center. *Leaves* 2-foliolate, sometimes with a tendril; leaflets more or less elliptic, acute, the base broadly

cuneate to rounded, 8.2–12.2 cm long and 4.4–8.6 cm wide, membranaceous to chartaceous, secondary veins 4–5 on a side, pubescent with scattered simple trichomes above, beneath with simple trichomes at least on the nerves, sometimes glabrescent, with axillary recesses beneath, these fringed with short trichomes, usually with a few large plate-shaped glands along lower part of midvein, drying olive to reddish-brown above, greenish-brown to olive with reddish veins and veinlets beneath; tendril simple, 10–14 cm long; petiolules 1.2–2.8 cm long, petiole 2.0–2.9 cm long, short-puberulous. *Inflorescence* a terminal panicle, the branches appressed short-puberulous. *Flowers* with the calyx cupular, subtruncate, 5–6 mm long and 4–5 mm wide, 5-denticulate with teeth ca. 0.5 mm long, puberulous, usually drying pale pinkish; corolla magenta (*Stern et al.*), tubular-infundibuliform, 3.6–4.5 cm long and 0.8–1.2 cm wide at the mouth, the tube 2.4–3.2 cm long, the lobes 0.8–1.2 cm long, puberulous on tube inside and on the lobes, tube inside mostly glabrous, pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, glabrous or pilose, usually reflexed forward from the base, 2.0–2.5 mm long, the connective apiculate ca. 0.5 mm, the longer filaments 1.6–1.7 cm long, the shorter filaments 1.1–1.2 cm long, the staminode 3–4 mm long, inserted 9–10 mm from base of corolla tube; pistil 2.3–2.4 cm long, the ovary cylindrical, densely minutely lepidote, 1.5–2 mm long and 1 mm wide, the ovules 4-seriate; disc pulvinate, 1 mm long and 1 mm wide. *Capsule* elongate-linear, 50–43 cm long and 0.9–1.0 cm wide, the valves somewhat compressed, with two submedian ridges and an inconspicuous median furrow between them, minutely warty but essentially glabrous; seeds thin, bialate, 0.8–0.9 cm long and 3–3.7 cm wide, body brown, wings hyaline membranaceous at the tips, brown at the base, indistinctly demarcated.

A liana of the tropical wet forest, this species was previously known only from Peru, Bolivia, and southern Brazil. The Panamanian collections extend its range northward and westward into the eastern Darien. *Cuspidaria floribunda* apparently flowers during the wet season from June to August.

This is one of the two Panamanian species of Bignoniaceae of which I have not seen living plants. It can be recognized in the herbarium by the color of its dried leaves: greenish-brown beneath with reddish brown veins and veinlets and reddish brown above. Its dried flowers superficially resemble those of *Xylophragma seemannianum*.

DARIÉN: Along Río Tuira between Río Pucro and Río Punusa, *Duke* 5386 (MO). Near Cana, *Stern et al.* 488 (GH, MO, US).

10. CYDISTA

Cydista Miers, Proc. Roy. Hort. Soc. 3: 191. 1863. TYPE: *C. aequinoctialis* (L.) Miers.

Levya Bur. *ex* Baill., Hist. Pl. 10: 28. 1888. TYPE: *L. nicaraguensis* Bur. *ex* Baill. = *Cydista aequinoctialis* var. *hirtella* (Benth.) A. Gentry.

Lianas, stems with 8 phloem arms in cross section; branchlets terete to tetragonal, without interpetiolar glandular fields; pseudostipules foliaceous or

absent. *Leaves* simple or 2-foliolate, sometimes with a simple tendril. *Inflorescence* an axillary or terminal raceme or few-flowered panicle. *Flowers* with the calyx cupular, truncate or irregularly and shallowly bilabiate, lepidote to puberulent or sub-hirsute; corolla white to magenta, tubular-infundibuliform, somewhat lepidote and sometimes inconspicuously puberulent outside; anthers glabrous, the thecae straight, divaricate; pollen grains single, acolpate, the exine finely reticulate; ovary narrowly cylindric, lepidote or somewhat puberulous, the ovules 2-seriate in each locule. *Fruit* a compressed, linear capsule, the valves parallel to the septum, the midline inconspicuous; seeds flat, bialate, the wings thin, brown, sometimes sub-hyaline at the extreme tip, not differentiated from the seed body.

Four species ranging from Mexico and the West Indies to Brazil.

a. Pseudostipules persistent, foliaceous, conspicuous; branchlets acutely tetragonal; capsule valves thin, uniformly flattened ..... 2. *C. diversifolia*

aa. Pseudostipules absent or inconspicuously foliaceous but then early caducous and present only on very young branchlets; branchlets not acutely tetragonal; capsule valves with margins raised or with submarginal ridges.

b. Calyx shallowly 2–3-labiate; branchlets terete; leaves simple or 2-foliolate, the leaf or leaflets conspicuously 3-veined from the base, beneath with glandular fields only in the axils of the basal pair of nerves; capsule with 2 parallel submarginal ridges ..... 3. *C. heterophylla*

bb. Calyx more or less truncate; branchlets terete to tetragonal; leaves 2-foliolate (except on seedlings), the leaflets more or less pinnately veined from the base, beneath with glandular fields in the axils of many secondary nerves; capsule with only the margins somewhat raised ..... 1. *C. aequinoctialis*

1. **Cydista aequinoctialis** (L.) Miers, Proc. Roy. Hort. Soc. 3: 191. 1863.

Bignonia aequinoctalis L., Sp. Pl., ed. 1. 2: 623. 1753. TYPE: (not seen).
B. spectabilis Vahl, Symb. Bot. 80. 1794. TYPE: collector unknown "ex India" (C, P-JU).
B. villosa Vahl, Eclog. Amer. 2: 44. 1798, pro parte. TYPE: Colombia, Santa Marta, *Von Rohr 21* (C, flower only).
B. picta H.B.K., Nov. Gen. Sp. Pl. 3: 136. 1819. TYPE: Venezuela, Orinoco, *Humboldt & Bonpland 1078* (P).
B. hostmannii E. Meyer, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 779. 1825. TYPE: Martinique, *Sieber s.n.* (M, W).
B. variabilis Sieber *ex* E. Meyer, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 779. 1825, pro syn., non Jacq.
B. sarmentosa Bertol., Fl. Guatimal. 25. 1840. TYPE: Guatemala, Escuintla, *Velasquez s.n.* (BOLO, fide Sandw.).
B. incarnata Aubl. sec. Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 7. 1842, non Aubl.
B. sarmentosa Bertol. var. *hirtella* Benth., Bot. Voy. Sulphur 128. 1844. TYPE: Nicaragua, Realejo, *Hinds s.n.* (K).
B. nitidissima DC., Prodr. 9: 160. 1845. TYPE: Venezuela, Caracas, *Vargas 244* (G-DC).
Temnocydia aequinoctialis (L.) Mart. *ex* DC., Prodr. 9: 155. 1845, pro syn.
T. spectabilis (Vahl) Mart. *ex* DC., Prodr. 9: 155. 1845, pro syn.
Cydista amoena Miers, Proc. Roy. Hort. Soc. 3: 191. 1863. TYPE: San Domingo [Hispaniola?], *Jussieu s.n.* (not seen, fide Knuth, Fedde Repert. Beih. 43: 636. 1928).
C. incarnata sensu Miers, Proc. Roy. Hort. Soc. 3: 191. 1863, non Aubl.
C. sarmentosa (Bertol.) Miers, Proc. Roy. Hort. Soc. 3: 191. 1863.
C. seemannii Miers, Proc. Roy. Hort. Soc. 3: 192. 1863, nomen nudum. TYPE: Panama, *Seemann 397* (BM).
C. spectabilis (Vahl) Miers, Proc. Roy. Hort. Soc. 3: 191. 1863.
Levya nicaraguensis Bur. *ex* Baill., Hist. Pl. 10: 29. 1888. TYPE: Nicaragua, *Levy 38* (F, fragments; K, fragments; P).

Arrabidaea guatemalensis K. Schum. & Loes., Bot, Jahrb. Syst. 23: 129. 1896. TYPE: Guatemala, *Bernoulli & Cario 2056* (K).
A. pseudochica Kränzl., Fedde Repert. 17: 19. 1921. TYPE: Mexico, El Platano, *Langlassé 137* (K).
Anemopaegma tonduzianum Kränzl., Fedde Repert. 17: 116. 1921. TYPE: Costa Rica, Guanacaste, *Tonduz 13912* (K, P).
Cydista pubescens Blake, Contr. U. S. Natl. Herb. 24: 23. 1922. TYPE: Honduras, Copán, *Pittier 8488* (US).
Arrabidaea isthmica Standl., Jour. Washington Acad. Sci. 15: 461. 1925, pro parte. TYPE: Panama, Canal Zone, *Pittier 2576* (leaves only) (US, holotype; GH, MO, NY, isotypes).

Liana to at least 8 cm in diameter, the bark gray to brownish gray, fibrous with longitudinal striation; stem with 8 phloem arms in cross section; branchlets subtetragonal to strongly tetragonal, usually drying dark, glabrous to pubescent, the nodes without interpetiolar glandular fields, sometimes with a ridge between opposite petioles; pseudostipules usually lacking or inconspicuous, occasionally thick-foliaceous but early deciduous on young twigs. *Leaves* 2-foliolate, sometimes with a tendril; leaflets more or less ovate, acuminate to obtuse, broadly cuneate to truncate, 5.4–16.2 cm long and 2.2–9.2 cm wide, membranaceous to chartaceous, secondary veins (3–)4–7(–8), lepidote above and beneath, variously pubescent with simple trichomes, especially along main veins beneath and with glandular fields in the axils of many secondary nerves, drying olive to brownish olive or reddish, shiny; tendril simple, 4–21 cm long; petiolules and petioles lepidote to pubescent, the petiole apex normally puberulent even in otherwise glabrous leaves, 0.8–3.9 cm long, petiole 0.9–4.5 cm long. *Inflorescence* a terminal or axillary panicle, its branches lepidote to simple pubescent. *Flowers* sweetly aromatic, calyx cupular, truncate to weakly 5-lobed or bilabiate, 4–10 cm long and 4–9 cm wide, lepidote to simple pubescent, sometimes with glands; corolla white or lavender with 13 maroon lines at the base of the lobes, 3 extending into the upper throat, the throat opening yellow, tubular-campanulate, 2.5–7.6 cm long and 0.6–2.2 cm wide at the mouth, the tube 1.9–5 cm long, lobes 0.6–2.6 cm long, glandular lepidote outside, inside simple puberulous with short, thick, 1–3-celled trichomes on the lobes, sparsely glandular-lepidote on the tube and simple-pubescent with multicellular trichomes from the level of stamen insertion to the base of the corolla tube; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 1.1–1.7 cm long, the shorter filaments 0.7–1.4 cm long, the staminode 3.5 mm long, inserted 4–5 mm from the base of the corolla tube; pistil 1.6–3.2 cm long, the ovary narrowly cylindrical, 2–3 mm long and 1 mm wide, lepidote, the ovules 2-seriate in each locule; disc obsolete. *Capsule* linear, round-tipped, flattened, 21–43 cm long and 1.4–2.4 cm wide, the margins rounded, slightly raised, the surface longitudinally finely wrinkled, lepidote, drying blackish; seeds 1.6–1.9 cm long and 5.0–7.3 cm wide, the wings membranaceous, brown, not demarcated from the seed body.

Most abundant in tropical moist forest where it is one of the commonest species of Bignoniaceae, *C. aequinoctialis* also occurs in tropical dry forest and premontane moist forest. It is a highly polymorphic and widespread species which ranges from Mexico and the West Indies to Brazil. It flowers and fruits throughout the year.

Field characteristics include the more or less tetragonal twigs, glandular fields in the axils of most main lateral nerves beneath, lack of pseudostipules (except occasionally on very young and actively growing branches), and more or less ovate leaflets (not strictly elliptic as in *Clytostoma*).

The pubescent-leaved form often referred to as *C. sarmentosa* or *C. pubescens* should be known as *C. aequinoctialis* var. *hirtella* (Benth.) A. Gentry.

BOCAS DEL TORO: SW of Bocas at Macaw Hills, *von Wedel 554* (MO). Fish Creek lowlands, *von Wedel 2388* (GH, MO, US). Fish Creek hills, *von Wedel 2415, 2449* (both GH, MO, US), *2451* (GH, US). Isla Colón, *von Wedel 2827* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Aviles X-1, X-8* (both F, MO); *Bailey & Bailey 132, 610* (both F); *Bangham 422* (A), *605* (A, F); *Blum & Dwyer 2130* (MO, SCZ); *Croat 4764* (MO), *5119, 5162, 5208* (all MO, SCZ), *5439* (MO), *5589, 5611* (both MO, SCZ), *5700, 6143* (both MO), *6155, 6169* (both MO, SCZ), *7176* (MO), *8310, 8552* (both MO, NY, SCZ), *8755, 9514, 9566* (all MO, SCZ), *10324* (MO), *11097* (MO, SCZ), *11610* (MO), *12268* (NY), *12645, 12957* (both MO), *13487* (MO, SCZ); *Dodge 3507* (GH, US); *Ebinger 288* (MO, US); *Foster 933* (PMA); *Hayden 20* (MO); *Kenoyer 533* (US); *Knight 69-87* (MO, SCZ); *Shattuck 784* (F), *1040, 1147* (both F, MO). Mojinga swamp near mouth of Río Chagres, *Allen 858* (F, GH, K, MO, NY, US). Near Gamboa, *Allen 1964* (F, GH, MO, NY, US). Near Madden Dam, *Alston 8865*, pro parte (BM), *8865* (K). Between Mt. Hope and Santa Rita trail, *Cowell 78* (NY). Mindi, *Cowell 189* (NY). Summit Garden, *Croat 12796* (MO). Near beach at Ft. Kobbe, *Duke 4696* (MO). Road C-21, *Duke 5777* (MO). France Field U. S. Army Tropic Test Mine Emplacement, *Dwyer 8528* (MO). Pipeline Road, *Gentry 1583* (MO). Near Venado beach, *Gentry 1604* (MO). Boy Scout road near Madden Lake, *Gentry 2055* (MO). Pipeline Road, *Gentry & Dwyer 3390* (MO). Near Margarita, *Gentry & Dwyer 4327* (MO). Road to Galeta Lab, *Gentry & Tyson 4854* (MO). Near Gatún, *Goldman 1861* (US). Panama Station, Panama Railroad, *Hayes 412*, pro parte (BM, K). Gatún, *Hayes 587, 590* (both NY). Mt. Hope, *Heriberto 40* (US). Summit Gardens, *Higgins 203, 207* (both MO, US). Road C-10, *Lazor 5460* (SCZ). Near Fort Randolph, *Maxon & Harvey 6533* (US). Along Río Indio de Gatún, *Pittier 2773* (BM, GH, NY, US). Las Sabanas, *Pittier 6762*, pro parte (BM, F, GH, MO, NY, US). Near Fort Randolph, *Standley 28628, 28642* (both US). Vicinity of Fort Sherman, *Standley 31183* (MO, US). Near Curundu, *Tyson 1089* (MO, SCZ). CHIRIQUÍ: West of San Bartolo Limite near Costa Rican border, *Croat 22192, 22159* (MO). Vicinity of Puerto Armuelles, *Woodson & Schery 811A* (MO). COCLÉ: Vicinity of El Valle de Antón, *Allen 1780* (F, GH, MO, NY, US), *2503* (US); *Bro. Paul s.n.* (US). Vicinity of Penonomé, *Williams 228* (NY, US). COLÓN: Miguel de la Borda, *Croat 9846* (MO). Nuevo Chagres, *Lewis et al. 1865* (GH, MO). Near Fort San Lorenzo, *Quistgaard 58* (PMA). Without locality, *Carrasquilla & Taymes 140* (MO). DARIÉN: 1–5 mi. downstream from El Real, *Duke 4922* (MO). Along Río Pirre, *Duke 4978* (GH, MO, US). Along Río Chucunaque between El Real and Río Canalones, *Duke 4989* (GH, MO). Santa Fé, *Duke 14256* (K, MO). Punto Sabanas opposite La Palma, *Gentry 3957* (MO). S of Jaqué, *Gentry 4116* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4410* (MO). El Real, *Gentry 4564, 4580* (both MO); *Stern et al. 755* (GH, MO, US). Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 882* (GH, K, MO, US). HERRERA: E of Las Minas, *Gentry 3138, 3144* (MO). S of Los Pozos, *Tyson 2683* (MO, SCZ). LOS SANTOS: Punta Mala, *D'Arcy & Croat 4215* (MO). PANAMÁ: Vicinity of Bejuco, *Allen 2458* (US). Cerro Campana, *Allen 2641* (MO). Vicinity of La Chorrera, *Allen 3646* (GH, MO, NY). Cerca de Río Tapía como 2 km de la carretera de Tocumen, *Correa & Escobar 1788* (MO). Between Capira and Chorrera, *Dodge 10715* (F, GH, MO). Between El Llano and Río Mamoní, *Duke 5531* (MO, US). Tocumen Agronomy School Farm, *Dwyer 4045* (MO, US), *5130* (MO). San José Island, *Erlanson 485* (GH, NY, US). Along road to Chepo, *Garner 4* (MO). Between El Llano and Cañitas, *Gentry 1414* (MO). Mouth of Río Pasiga, *Gentry 2198* (MO). Río Pasíga, *Gentry 2267* (MO). Río Agua Clara, *Gentry 2629* (MO). Near Río Espavé, *Gentry 3711* (MO). 0–4 mi. from Río Bayano crossing on road to Santa Fé, *Gentry 3859* (MO). W of Chepo, *Gentry 4970* (MO); *Gentry & Tyson 1642* (MO). Dam site on Río Bayano, *Gentry & Tyson 1663D* (MO). Las Sabanas, *Paul 236* (US). Near Panama City, *Seemann 397* (K). Taboga Island, *Standley 27944* (US). Vicinity of Campana, *Woodson et al. 1309* (A, MO, NY). Between Pacora and Chepo, *Woodson et al. 1651* (A, MO, NY). Vicinity of Campana, *Woodson et al. 1679* (A, MO, NY).

SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1477* (MO). Outskirts of Puerto Obaldía, *Gentry 1570* (MO). VERAGUAS: Santiago, *Dwyer & Kirkbride 7438* (MO). Coiba Island, *Seemann 602* (K). Island off Veraguas, *Sinclair s.n.* (K). Between Soná and Santiago, *Woodson et al. 1196* (A, K, MO, NY). Without locality, *Hinds s.n.* (K). WITHOUT LOCALITY: *Duchaissaing s.n.* (K); *Duke 12268* (MO).

2. **Cydista diversifolia** (H.B.K.) Miers, Proc. Roy. Hort. Soc. 3: 192. 1863.

Bignonia diversifolia H.B.K., Nov. Gen. Sp. Pl. 3: 133. 1819. TYPE: Mexico, Campeche, *Humboldt & Bonpland s.n.* (P).
Anemopaegma vargasianum DC., Prodr. 9: 190. 1845. TYPE: Venezuela, Caracas, *Vargas s.n.* (G-DC).
Bignonia sagreana DC., Prodr. 9: 148. 1845. TYPE: Cuba, *Sagra s.n.* (G-DC, K).
Cydista vargasiana (DC.) Miers, Proc. Roy. Hort. Soc. 3: 192. 1863.
Pleonotoma diversifolium (H.B.K.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 274. 1897.

Liana to at least 5 cm in diameter, the bark smooth, striate vertically; stem with 8 phloem arms in cross section; branchlets sharply tetragonal with angles ribbed, lepidote to simple pubescent, the nodes without interpetiolar glandular fields; pseudostipules foliaceous, 4 at each node, 0.7–1.5 cm long and 0.6–1.7 cm wide. *Leaves* 2-foliolate, at times cirrhose, sometimes simple, especially the first leaves on a shoot which then intergrade with pseudostipules; leaflets ovate, acuminate, basally truncate to shallowly cordate, 4.0–11.6 cm long and 2.2–8.5 cm wide, entire, membranaceous, basally palmately 5-veined, the secondary veins 3–4 on a side, the surface with scattered lepidote scales, otherwise glabrous or simple-puberulent on main veins above and beneath, sometimes sparsely puberulent overall beneath, conspicuous plate-shaped glands in the axils of basal nerves beneath, drying olive with the venation beneath often reddish; tendril simple, 4–13 cm long; petiolules 1.1–2.2 cm long, the petiole 1.4–3.6 cm long, (to 5 cm on simple leaves), lepidote to simple puberulous, the simple trichomes often with curved tips. *Inflorescence* an axillary or terminal panicle, the branches lepidote. *Flowers* with an inconspicuous sweet aroma, calyx cupular, 5-lobed to more or less truncate, 3–5 mm long and 4–6 mm wide, lepidote, slightly puberulous at least around the margin; corolla magenta, the throat white inside, tubular-campanulate to tubular-infundibuliform 2.4–3.9 cm long and 0.8–1.8 cm wide at the mouth, the tube 1.6–2.6 cm long, the lobes 0.7–1.2 cm long, lepidote and puberulous outside at least on the lobes, within glandular-lepidote on the lobes and sparsely so in the throat, glandular simple-pubescent at and below the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2–2.5 mm long, the longer filaments 1.1–1.4 cm long, shorter filaments 0.8–1.1 cm long, the staminodes 3–5 mm long, inserted 2–3 mm from base of the corolla tube; pistil 1.9–2.1 cm long, the ovary cylindric, 3–5 mm long and 1.5 mm wide, lepidote and inconspicuously puberulous, the ovules 2-seriate; disc lacking. *Capsule* linear, strongly compressed, 30–40 cm long and 1.2–1.5 cm wide, inconspicuously lepidote or lepidote-punctate; seeds 1.2–1.3 cm long and 4–5.5 cm wide, the wings membranaceous, brown, not differentiated from the seed body.

An extremely common species of the tropical dry forest, this plant also occurs in premontane moist and less commonly in tropical moist forests. In the tropical moist forest it appears to be restricted to edaphically dry locations, *e.g.* the only

Panamanian locality is a dry limestone cave area near Madden Lake. The species ranges from Mexico to Venezuela and the West Indies. It flowers mostly during the wet season from May through September, also blooming sporadically in the dry season. Seeds are mostly released during the early dry season and are wind dispersed.

This species is distinctive in its conspicuously square stem with ribbed angles and conspicuous foliaceous pseudostipules. Glandular fields in the axils of the basal pair of lateral nerves of the leaf undersurface are also a useful character.

CANAL ZONE: Boy Scout road, *Gentry 2480* (MO). Alrededores de la Represa Madden, *Kant 1* (MO, PMA). PANAMÁ: Archaeological site near Madden Lake, *Gentry 5012* (MO).

3. **Cydista heterophylla** Seib., Carnegie Inst. Washington Publ. 522: 417. 1940. TYPE: Mexico, Yucatan, *Lundell & Lundell 7350* (A, F, US).—FIG. 10.

Bignonia lepidota Seem., Bot. Voy. Herald 179. 1854, non H.B.K. SYNTYPES: Panama, Isla de Iguana, *Seemann 601* (BM, K); *Cuming 1262*, pro parte (K).

Liana to at least 5 cm in diameter, the bark smooth, gray; stem with 8(–16) phloem arms in cross section; branchlets terete to subterete, grayish with inconspicuous lenticels, lepidote when young, glabrous when older, the nodes lacking interpetiolar glandular fields, sometimes with a ridge connecting opposite petioles; pseudostipules lacking. *Leaves* simple or 2-foliolate, sometimes cirrhose, the leaves of young branches characteristically simple and appearing in a whorl of 4 due to suppression of an internode; blades ovate to obovate, acute to acuminate, truncate to subcordate, 4.5–17.5 cm long and 2.1–11.1 cm wide, membranaceous to chartaceous, secondary veins 3–5 on a side, the basal pair strongly arcuate and arising from the base, the surface minutely papillate, scattered lepidote above and beneath, the scales sometimes deciduous, usually minutely scabrous on main veins, glandular fields in the axils of the basal pair of lateral nerves beneath, typically drying olive to yellowish-olive beneath with brownish reticulate venation at least when young, darker above; tendril simple, 8–18 cm long; petiole and petiolules lepidote to scabrous, the petiolules 0.5–5.1 flowers, usually borne when leafless, the branches lepidote. *Flowers* somewhat aromatic, calyx cupular, 4–7 mm long and 4–6 mm wide, shallowly bilabiate to 3-lobed, rarely truncate with the tip calypterate, the edge often drying lighter, lepidote, sometimes with plate-shaped glands; corolla lavender to deep magenta inside and on the lobes, the tube white inside and at base of the 2 adaxial lobes with ca. 13 magenta nectar guides in the floor, tubular-campanulate to tubular-infundibuliform, slightly bilibiate, 4–5.9 cm long and 1.1–1.7 cm wide at the mouth of tube, the tube 2.8–3.7 cm long, the lobes 0.9–1.9 cm long, inconspicuously lepidote outside, more so inside, simple-puberulous on the lobes, especially inside, puberulous with short sometimes gland-tipped trichomes at the level of stamen insertion; stamens didyna-

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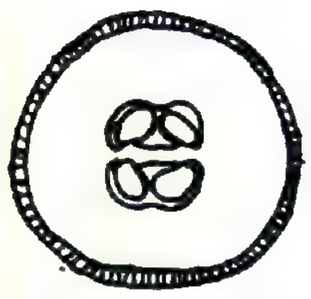
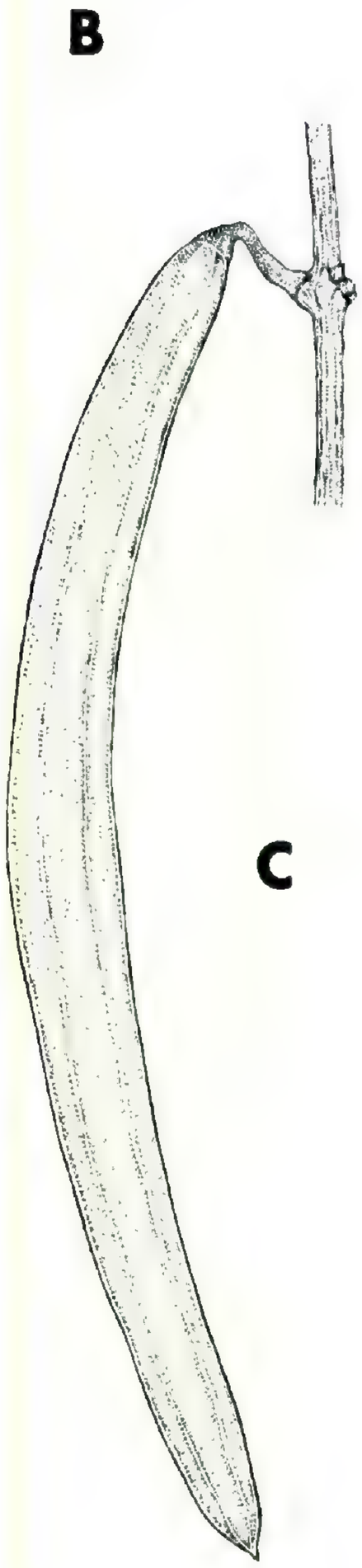
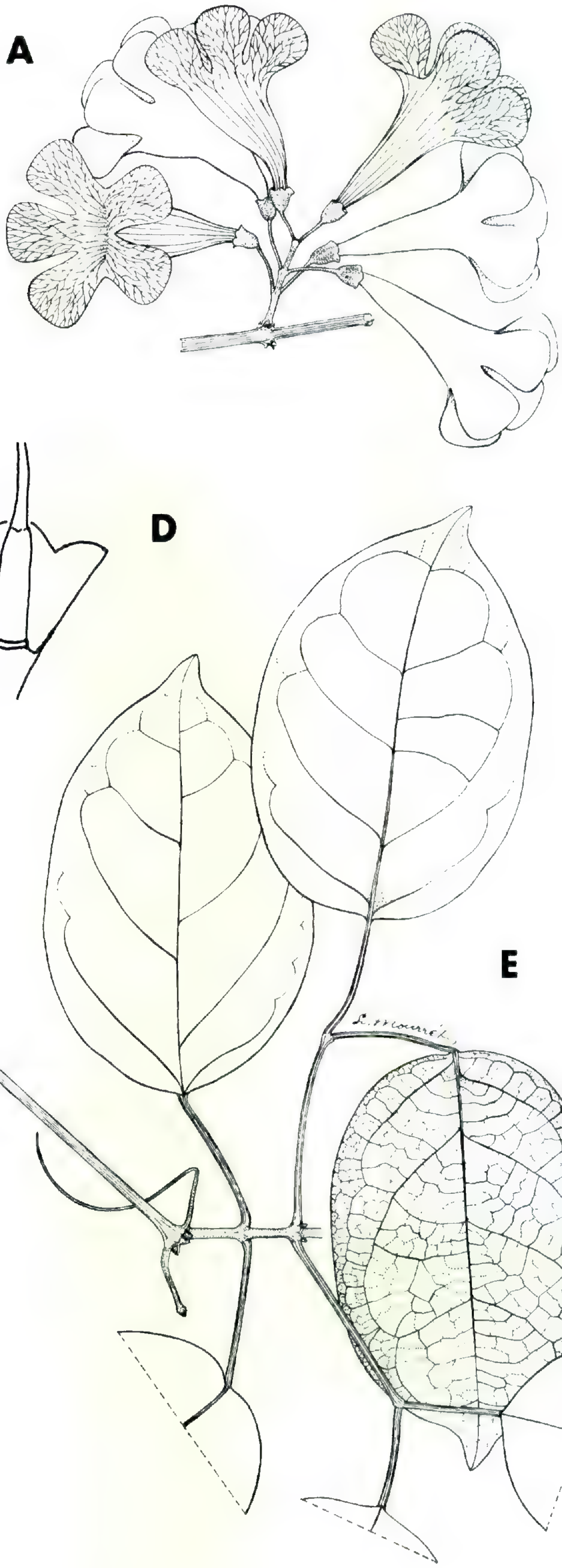
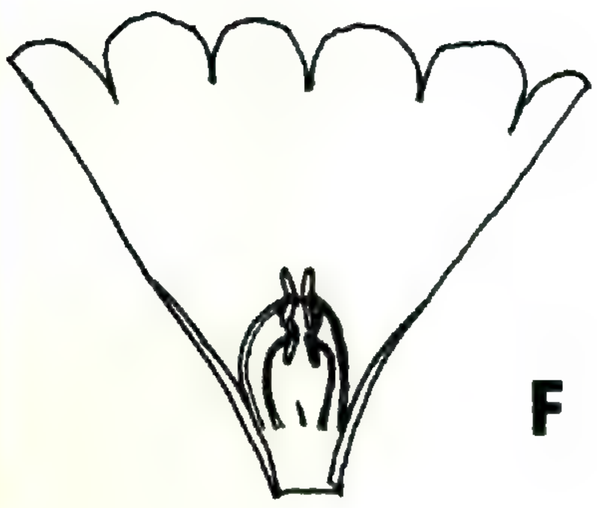
FIGURE 10. *Cydista heterophylla* Siebert.—A. Inflorescence (× ½).—B. Ovary cross section (× 12). [After *Gentry 4967* (MO).]—C. Fruit (× ½). [After *Gentry 4088* (MO).]—D. Ovary (× 2½).—E. Habit (× ½). [After *Gentry 4088* (MO).]—F. Corolla split open (× ⅗). [After *Gentry 4967* (MO).]









mous, the anther thecae divaricate, 4–5 mm long, the longer filaments 1.7–1.8 cm long, the shorter filaments 1.1–1.2 cm long, the staminode 4 mm long, inserted 4–5 mm from the base of the corolla tube; pistil 3.0–3.1 cm long, the ovary linear, lepidote, 4–5 mm long and 1.5 mm wide, the ovules 2-seriate in each locule; disc reduced to glandular tissue at base of ovary. *Capsule* linear, flattened but with 2 conspicuous raised longitudinal submarginal ridges on each valve, rounded at the tip, 11–33 cm long and 1.0–2.0 cm wide, the surface glabrous to more or less lepidote; seeds 0.8–1.5 cm long and 2.6–5.3 cm wide, the wings membranaceous, merging into the seed body, brown with irregularly hyaline tips.

A common vine of the tropical dry forest and drier parts of the tropical moist forest, this species occurs also, but uncommonly, in moister parts of the tropical moist forest. It ranges from Mexico to Colombia. It flowers during the dry season especially in April and May. The species is deciduous during the blooming period so leaves are rare in herbaria.

A propensity to simple leaves and a strongly arcuate basal pair of lateral nerves with glandular fields in their axils on the undersides mark this species. An additional field character, especially useful on juvenile plants, is the two terminal pairs of simple leaves which appear as a whorl of four.

CANAL ZONE: Barro Colorado Island, *Croat 5426* (MO), *8206* (MO, SCZ), *Shattuck 784*, pro parte (F, MO). Victoria Fill near Miraflores Locks, *Allen 1756* (GH, MO). Near Madden Dam, *Alston 8865*, pro parte (BM, K); Gaillard Highway 1 mi. NW of Summit, *Croat 9776* (MO, NY, SCZ). Near Madden Dam, *Dodge 16570* (MO, U). Road K-19, *Gentry 1779* (MO). N of Summit, *Gentry 5126* (MO). Paraíso, *Hayes 126* (BM, K). Las Sabanas, *Pittier 6762*, pro parte (BM, GH, MO, NY). Cocoli Road, *White 146* (GH, MO). DARIÉN: Isla Encanto in Golfo de San Miguel, *Gentry 4020* (MO). Near Punta Alegre, *Gentry 4059* (MO). Punta Sabanas across bay from La Palma, *Gentry 4088* (MO). Ridge from Cerro Pavarandó to Cerro Derumba, *Gentry 4206* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4420* (MO). El Real, *Gentry 4539, 4575* (both MO). HERRERA: E of Las Minas, *Gentry 3143* (MO). PANAMÁ: E of El Llano, *Croat 14482* (MO), *14499* (MO, SCZ). San José Island, *Erlanson 38* (GH, US). Río Pasiga, *Gentry 2204, 2256, 2274, 2359* (all MO). Río Maestro, *Gentry 2219* (MO). Río Piragua (Tabardi), *Gentry 2564* (MO). Icantí, *Gentry 2615* (MO). Near Río Espavé, *Gentry 3700* (MO). 16 km from Bayano crossing on trail to Santa Fé, *Gentry 3817* (MO). 1 mi. W of Cañitas, *Gentry 4967* (MO). San José Island, *Johnston 812* (BM, GH, MO, US), *831* (GH). Juan Díaz, *Maxon & Harvey 6640*, pro parte (US). Chepo, *Pittier 4766* (JS). Perlas Islands, El Rey Island, *Svenson 417* (GH). WITHOUT LOCALITY, *Cuming 1262* (K); *Seemann 601* (BM, K).

11. DENDROSICUS

Dendrosicus Raf., Sylva Tell. 80. 1838. TYPE: *D. saxatilis* Raf. = *D. latifolius* (Mill.) A. Gentry.

Amphitecna Miers, Trans. Linn. Soc., ser. 1. 26: 163. 1870. TYPE: *A. macrophylla* (Seem.) Miers *ex* Baill. = *Dendrosicus macrophyllus* (Seem.) A. Gentry.

Crescentia sect. *Enallagma* Miers, Trans. Linn. Soc., ser. 1. 26: 174. 1870.

Enallagma (Miers) Baill., Bull. Soc. Linn. Paris 85: 679. 1887. TYPE: *E. cucurbitina* (L.) Baill. = *Dendrosicus latifolius* (Mill.) A. Gentry.

Small to medium-sized *trees*. *Leaves* simple, alternate, borne singly on the twigs. *Inflorescence* a solitary flower or a few-flowered terminal fascicle cauliflorous on bracteate short-shoots from older twigs and branches. *Flowers* with the calyx large, rupturing irregularly, usually bilabiate, sometimes subtruncate,

rarely spathaceous; corolla greenish-white, tubular-campanulate, usually with an inconspicuous transverse fold in the throat, thick; stamens subexserted, the anthers glabrous, the thecae thick, somewhat divergent; pollen grains single, ecolpate, the exine microreticulate; ovary ovoid-elliptic, more or less lepidote, incompletely 2-locular. *Fruit* a pepo or calabash, spherical to ellipsoidal, indehiscent, with a relatively fragile woody shell and soft pulp; seeds thick, large, more than 1.3 cm long and 1.4 cm wide, not winged, embedded in the pulp.

About ten species ranging from Mexico and the West Indies to coastal Venezuela and Ecuador. The species of *Dendrosicus* are readily distinguished from most other members of the family by their large, simple, mostly alternate leaves.

The use of the name *Dendrosicus* for this genus is discussed by Gentry (1973).

Useful references:

Gentry, A. H. Studies in Bignoniaceae VII. *Dendrosicus*, *Enallagma*, and *Amphitecna*, Taxon 22: 643–646. 1973.

Williams, L. O. *Amphitecna* and *Enallagma*. Fieldiana, Bot. 36: 21–27. 1973.

a. Fruit spherical; leaves coriaceous; occurring near sea level ..... 3. *D. latifolius*
aa. Fruit ellipsoidal, apiculate; leaves chartaceous; generally occurring above 100 m elevation.
  b. Calyx thick, irregularly and shallowly split; flowers mostly terminal; ovary bilocular to above the middle; leaves drying gray or brownish with darker midvein, without a fine network of impressed veinlets, not shagreened; over 1000 m elevation ..... 4. *D. sessilifolius*
  bb. Calyx thin, split to near the base; flowers terminal or on bracteate short shoots from older branches; ovary unilocular except at the extreme base or bilocular to above the middle; leaves drying gray or olive with lighter midvein, often with a fine network of impressed whitish veinlets and more or less shagreened; under 1000 m elevation.
    c. Calyx bilabiately split; buds round-tipped.
      d. Flowers cauliflorous on bracteate short shoots; ovary unilocular except at the extreme base; Atlantic slope ..... 2. *D. kennedyi*
      dd. Flowers mostly terminal; ovary bilocular to above the middle; Pacific slope ..... 1. *D. isthmicus*
    cc. Calyx spathaceously split; buds pointed ..... 5. *D. spathicalyx*

1. **Dendrosicus isthmicus** A. Gentry, Phytologia 26: 442. 1973. TYPE: Panamá, Chiriqui, *Liesner 75* (MO).

Small *tree* to 10 m. *Leaves* simple, alternate, glabrous, narrowly elliptic, acute to acuminate, basally cuneate, 7–32 cm long and 2.8–10 cm wide, the midrib raised beneath, the main veins drying whitish or yellowish beneath, leaf surface gray or olive-gray above and beneath, the veinlets sometimes minutely appressed beneath; the petiole less than 5 mm long or lacking. *Inflorescence* of 1–2 flowers, usually terminal, the pedicel 2–4 cm long. *Flowers* with the calyx bilabiately split almost to the base, 2.3–3 cm long, each lobe 1.3–1.8 cm wide, obtuse, glabrous with a few plate-shaped glands; corolla greenish white, 3.4–6 cm long and 1.7–2 cm wide at the mouth, the tube 2.4–3.5 cm long, glabrous, the rim lepidote papillate, the lobes fused into a reflexed rim; stamens subexserted, the anther thecae divergent, each 4–5 mm long and 1–2 mm wide; filaments 2–3 cm long, inserted ca. 1.5 cm from the base of the tube; pistil ca. 4 cm long, the

ovary oblong, 2–3 mm long and ca. 2 mm wide, glandular lepidote, 2–locular in the lower ⅔ with the ovules several seriate on 2 indistinct axillary placentae in each locule, above unilocular with parietal placentation; disc annular pulvinate. *Fruit* a pepo or calabash, to 14 cm long and 7 cm wide, ellipsoid, apiculate at the ends with thick seeds embedded in the pulp.

This species is apparently restricted to the tropical wet forest of eastern Costa Rica and western Panama. It has been collected only on the Pacific side of the Cordillera Central.

The status of this species is difficult to evaluate from the limited material available. Most of the collections have only a single flower, and the only mature fruit was found washed up on a beach. These specimens were originally determined as *Enallagma latifolia* (= *Dendrosicus latifolius*), although they appear more closely related to *D. sessilifolius*. *Dendrosicus isthmicus* differs from *D. latifolius* in leaf shape and texture, fruit shape, and especially in ecology. It differs from *D. sessilifolius* in its generally smaller, narrowly elliptic rather than oblanceolate to narrowly obovate leaves, as well as in the characters noted in the key. Athough differences in calyx thickness and degree of splitting are relative, they appear to be constant. The uneven splitting and thickness of the calyx of *D. sessilifolius* usually results in a whitish edging along the split edges of its black-drying calyx especially near the base of the splits; in *D. isthmicus* the thinner calyx lacks a whitish edging along the lines of rupture.

The closest relative of *D. isthmicus* is *D. kennedyi*, and I am unable to separate these species reliably on the basis of sterile or fruiting material. Terminal (noted as terminal or cauline on one collection) placement of flowers, the blunt-tipped calyx, and geographic separation appear sufficient for separation of this species from *D. kennedyi*. In addition the leaves of *D. isthmicus* are usually much smaller and the ovary (based on a single dissection for each species) is bilocular to above the middle rather than only at the extreme base as in *D. kennedyi*.

CHIRIQUÍ: Progreso, *Cooper & Slater 277* (F, NY, US). San Bartolo de Limite, 21 km WNW of Puerto Armuelles, rich forest, 400 m, *Leisner 75* (MO). Burica Peninsula, Quebrada de Fraile, *Liesner s.n.* (MO). COCLÉ: El Valle, vicinity of La Mesa, 900 m, tropical wet forest, *Gentry 7443* (MO).

2. **Dendrosicus kennedyi** A. Gentry, Phytologia 26: 441. 1973. TYPE: Panama, Bocas del Toro, *Kennedy & Dressler 1258* (MO).—FIG. 11A–B.

Small *tree*. *Leaves* simple, alternate, glabrous or sparsely lepidote, oblanceolate to narrowly obovate, apically acute to acuminate, basally cuneate, attenuate, the petiole not differentiated, 16–38 cm long and 5–14 cm wide, the midrib conspicuously raised beneath, the main veins drying whitish beneath, leaf surface gray above and grayish beneath, the veinlets sometimes minutely impressed beneath. *Inflorescence* 1–2 flowers from a conspicuously bracteate abbreviated short-shoot on older branches or trunk, the pedicels 1.5–3 cm long. *Flowers* with the calyx bilabiately split almost to base, 1.5–3.0 cm long, each lobe ca. 1 cm wide, conspicuously apiculate; corolla greenish white, 4.3–4.8 cm long and 1.3–1.9

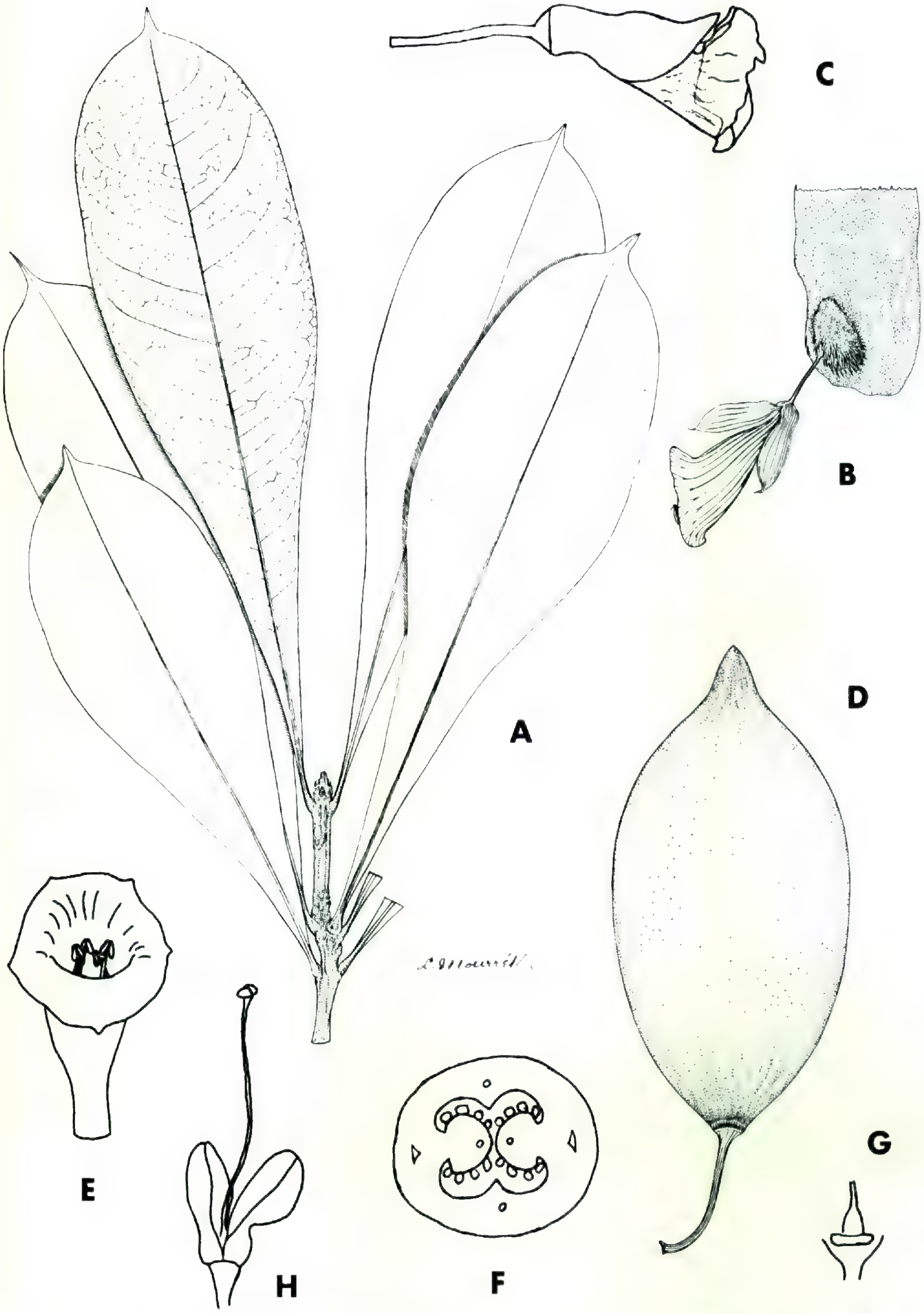


FIGURE 11. *Dendrosicus*.—A–B. *D. kennedyi* A. Gentry.—A. Habit (× 3/10).—B. Inflorescence (× 3/5). [After *Kennedy & Dressler 1258* (MO).]—C–G. *D. spathicalyx* A. Gentry.—C. Flower (× 3/5). [After *Gentry 5769* (MO).]—D. Fruit (× 1/2). [After *Dressler 3943* (MO).]—E. Corolla (× 3/5).—F. Ovary cross section (× 3/8).—G. Ovary and disc (× 1 1/5). [After *Gentry 5769* (MO).]—H. *D. latifolius* (Mill.) A. Gentry, calyx (× 3/5). [After *Gentry & Forero 7379*, Colombia (MO).]

cm wide at the mouth, the tube 2.7–3.5 cm long, the lobes fused into a reflexed rim; stamens subexserted, the anther thecae somewhat divergent, 4–5 mm long and 1.5–2 mm wide, the filaments 2.4–2.8 cm long, inserted 1.3–1.5 cm from the base of the tube; pistil ca. 4 cm long, the ovary rounded conical, 2–3 mm long and 2 mm wide, densely lepidote, the ovules several seriate on 2 parietal placentae; disc annular pulvinate. *Fruit* a pepo or calabash, 11.5–13 cm long and 5.5–7 cm wide, ellipsoid, apiculate at the ends with thick seeds 1.3–1.5 cm long embedded in the pulp.

This species is restricted to the tropical wet forest and premontane wet forest of Bocas del Toro Province and adjacent Costa Rica. It is distinguished from its congeners in Panama by its thin, sharply pointed, deeply bilabiate calyx. Among its closest allies are *D. isthmicus* and *D. macrophyllus* (Seem.) A. Gentry of Mexico and Guatemala. The former differs in the characters given in the key; the latter most conspicuously in its 8-costate rather than smooth fruit.

It is possible that the collections cited include a second species. The Kirkbride and Duke and the von Wedel collections have shorter leaves which are widest near the middle and may prove separable from *D. kennedyi*. These two collections are somewhat similar to material from the wet Pacific lowlands in Costa Rica and Panama described as *D. isthmicus*. Inadequate material prevents better evaluation of these collections.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 36* (US). Near Almirante, *Kennedy & Dressler 1258* (MO), 1261 (MO, PMA). Above Quebrada Hurón on Cerro Bonyic, *Kirkbride & Duke 615* (MO). Fish Creek mountains, *von Wedel 2258* (GH, MO).

3. **Dendrosicus latifolius** (Mill.) A. Gentry, Taxon 22: 644. 1973.—FIG. 11H.

Crescentia latifolia Mill., Gard. Dict., ed. 8. 306. 1768. TYPE: (not seen).
C. cucurbitina L., Mant. Pl. 2: 250. 1771. TYPE: Based on *C. latifolia* Mill.
C. lethifera Tussac, Fl. Antill. 4: 50, *tab. 17*. 1827. TYPE: (not seen).
C. toxicaria Tussac, Fl. Antill. 4: 50, *tab. 17*. 1827. TYPE: (not seen).
Dendrosicus saxatilis Raf., Sylva Tell. 80. 1838. TYPE: Based on *C. cucurbitina* L.
Crescentia obovata Benth., Bot. Voy. Sulphur 130. 1844. TYPE: Panama, Isle of Gorgona, *Barclay s.n.* (BM, K).
C. palustris Forsyth *ex* Seem., Bot. Voy. Herald 183. 1854, pro syn.
C. coriacea Miers, Trans. Linn. Soc. 26: 177. 1870. TYPE: Fruit and unpressed leaves, without data, *P. Browne*, Jamaica? (BM).
C. cuspidata Miers, Trans. Linn. Soc. 26: 178. 1870. TYPE: Venezuela, *Fendler 780* (K).
Enallagma cucurbitina (L.) Baill. *ex* Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 247. 1894.
E. obovata (Benth.) Baill. *ex* Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 247. 1894.
E. latifolia (Mill.) Small, Fl. Miami 171. 1913.
Amphitecna obovata (Benth.) L. O. Wms., Fieldiana, Bot. 36: 25. 1973.

Small scraggly *tree* to 10 m tall and 18 cm d.b.h., the branches usually crooked, the crown open; twigs subterete or 3- or 4-angled with decurrent ridges below the nodes. *Leaves* simple, alternate to subopposite, obovate, the tip rounded to almost acute, usually apiculate, the base cuneate-attenuate, 7–19 cm long and 3.3–10.6 cm wide, rigid-chartaceous to coriaceous, secondary veins 7–30 on a side, the midvein depressed above, glabrous beneath, with plate-shaped glands especially at the base, drying grayish olive to brownish, the petiole poorly defined, more or

less winged, 0.2–1.1 cm long, glabrous. *Inflorescence* a single flower or fascicle of 2–3 flowers borne on the larger twigs, pedicels glabrous, 2.2–3.6 cm long. *Flowers* with the calyx split into subequal anterior and posterior halves, 2.5–3.7 cm long and 1–2.5 cm wide, essentially glabrous; corolla greenish-white, tubular with a transverse fold midway across the lower side of throat, fleshy, 3.8–6.2 cm long and 1.2–2.4 cm wide at mouth, the tube 3.0–4.0 cm long, the lobes 0.8–1.5 cm long, upper 2 and lower 3 lobes respectively more or less fused, mostly glabrous, stalked-lepidote on the lobes outside and at the level of stamen insertion inside; stamens subexserted, the anther thecae thick, only partially divergent, 5–6 mm long, the anterior filaments 2.6 cm long and inserted 1.5–1.6 cm from base of tube, the posterior filaments 2.4–2.5 cm long, inserted 2 cm from base of tube, staminode ca. 10 mm long, inserted ca. 10 mm from base of tube; pistil 5.0–5.1 cm long, the ovary rounded-conical, 4–5 mm long and 3 mm wide, lepidote, the ovules ca. 4-seriate in each locule of the bilocular ovary; disc pulvinate, 2 mm long and 5 mm wide. *Fruit* a pepo or calabash, more or less spherical when mature, 6–9 cm in diameter, glabrous, minutely papillate with scattered sunken plate-shaped glands; seeds thick, corky, 1.3–1.6 cm long and 1.6–1.8 cm wide, without wings.

A common tree of seashores, mangrove fringes, and brackish water swamps along both coasts, *D. latifolius* ranges from southern Florida and Mexico through the West Indies to Venezuela. It flowers more or less throughout the year, especially in the wet season.

The fruits are reported by campesinos to be an important food source of the paca and the insipid pulp is eaten by humans in some localities. Fruits of *D. latifolius* are commonly found washed up on beaches with still fertile seeds which germinate only when the fruit is broken open. Evidently seed dispersal is a combination of water-dispersed fruit with mammal-dispersed seeds, either vector being sufficient to disseminate the species.

The large, simple, typically alternate leaves of *D. latifolius* are unusual in the Bignoniaceae. Their coriaceous texture and the presence of a definite petiole serve to distinguish this species from *D. sessilifolius*. The more or less spherical fruit is superficially similar to that of *Crescentia alata* but unlike the more elongate fruits of other species of *Dendrosicus*.

BOCAS DEL TORO: Isla Colón, *von Wedel 561* (GH, MO, U). Water Valley, *von Wedel 988* (GH, MO). Old Bank Island, *von Wedel 2101* (GH, MO, US). Johns Creek, *von Wedel 2769* (GH, MO, US). CANAL ZONE: Summit Garden, *Croat 13827* (MO, SCZ). Chagres, *Fendler 210* (K). 1 mi. NE of Piña, *Lewis et al. 1842* (MO). Along Río Indio de Gatún, *Pittier 2782* (US). Vicinity of Fort Sherman, *Standley 30919* (US); *Tyson & Blum 3797* (MO, SCZ). COLÓN: Vicinity of Camp Piña, *Allen 3632* (MO). 3 mi. SW of Colón along beach, *Croat 14168* (MO). W of Portobelo, *Gentry 1742* (MO). Aspinwall, *Hayes 862* (NY). Punta Pedro, Icacal between Salud and mouth of Río Indio, *Howell 40* (MO). Salud, *Lao & Holdridge 250* (MO). Río Indio de Fató, *Pittier 4272* (US). Plaza Colón, *Rose 22028* (US), *22078* (NY). DARIÉN: On Río Tuira ca. 3 mi. NW of El Real, *Duke 4820* (SCZ). S of Jaqué, *Gentry 4121* (MO). Along Río Tuira below El Real and Piriaque Island, *Stern et al. 891* (GH, K, MO). LOS SANTOS: Azuero Peninsula near Raja Point, *Ostenfeld 20* (C, US). Punta Mala, *Tyson 2738* (MO, SCZ). PANAMÁ: San José Island, *Erlanson 4* (GH, NY, US); *Harlow 97* (P, US); *Johnston 10, 1179* (both GH); *Stimson 5333* (NY, PMA, SCZ); *Tyson & Loftin 5074* (SCZ). Seaside, Panamá, *Hayes 826* (NY). SAN BLAS: Mulatupo, *Duke 8552*

(MO). Near Puerto Obaldía, *Pittier 4362* (US). VERAGUAS: Isla de Coiba, *Dwyer 1568* (MO); *Foster 1617* (PMA); *Kelsall 467* (K). WITHOUT LOCALITY: *Barclay s.n.* (BM, K); *Hayes 44* (GH).

4. **Dendrosicus sessilifolius** (Donn. Sm.) A. Gentry, Taxon 22: 646. 1973.

Tabebuia sessilifolia Donn. Sm., Bot. Gaz. (Crawfordsville) 25: 156. 1898. TYPE: Costa Rica, Tablazo, *Tonduz 7937* (BR, CR, US).

Neotuerckheimia gonoclada Donn. Sm., Bot. Gas. (Crawfordsville) 47: 259. 1909. TYPE: Costa Rica, San José, *Tonduz 7384* (BM, GH, K, M, MO, NY, US).

Enallagma sessilifolia (Donn. Sm.) Standl., Publ. Field Mus. Nat. Hist., Bot. ser. 18: 1120. 1938.

Amphitecna sessilifolia (Donn. Sm.) L. O. Wms., Fieldiana, Bot. 36: 25. 1973.

Shrub or *tree* to 18 m tall and 25 cm d.b.h.; twigs subterete, glabrate, usually moss-covered. *Leaves* simple, alternate, oblanceolate to narrowly obovate, acute, attenuate with the petiole undifferentiated and essentially lacking, 13–29 cm long and 4.0–8.5 cm wide, chartaceous, secondary veins 11–16 on a side, the midvein raised above, lepidote above and beneath, a few plate-shaped glands at base beneath, drying dark brown. *Inflorescence* a terminal fascicle, the pedicels glabrous to inconspicuously lepidote, 2.2–7.9 cm long, commonly reduced to a single flower. *Flower* with the calyx thick, fleshy, irregularly split into subequal anterior and posterior halves or merely ruptured apically by the expanding corolla, one of the lobes sometimes itself split, 2.5–2.8 cm long and 1.9–2.1 cm wide, glabrous; corolla greenish white, tubular, usually with an inconspicuous transverse fold in the throat, fleshy, 4.1–5.2 cm long and 1.2–1.6 cm wide at the mouth, the tube 2.5–3.3 cm long, the lobes fused, 0.5–1.2 cm long, glabrous; stamens subexserted, the anther thecae thick, somewhat divergent, 5 mm long and 2–3 mm wide, the anterior filaments 2.3–2.4 cm long, inserted 13–14 mm from base of tube, the posterior filaments 2.5–2.7 cm long, inserted 16–18 mm from base of tube, the staminode 2.5–2.7 cm long, inserted 16–18 mm from the base of the tube; pistil 3.8–3.9 cm long, the ovary rounded-conical, 8–9 mm long and 4–5 mm wide, incompletely 2-locular with 2 protruding, parietal placentae at the top, these fused above middle, the ovules then irregularly 4-seriate in each locule; disc pulvinate, ca. 3 mm long and 9–10 mm wide. *Fruit* a pepo or calabash, ellipsoidal with the apex elongated, 12–15 cm long and 6.6–7.2 cm in diameter, evenly rough-surfaced under a lens, inconspicuously scattered lepidote; seeds thick, 1.5–2 cm long and 1.5–2.4 cm wide, without wings.

A tree of the premontane rain forest and lower montane rain forest of Costa Rica and Panama, this species occurs from 1200–2000 m elevation. *Dendrosicus sessilifolius* flowers and fruits irregularly throughout the year.

The fruits are much softer-shelled than those of *D. latifolius*, probably reflecting elimination of water borne dispersal. It seems that mammals disperse the seeds by eating the pulp which surrounds them; the pulp of mature fruits is also eaten by campesinos in Chiriquí Province.

The leaves of *D. sessilifolius* can be told from those of *D. latifolius* by their less rigid texture and narrower shape; the ecology of the two species is also distinct. The ellipsoid, apiculate fruits of *D. sessilifolius* are different from the spherical fruits of *D. latifolius*. *Dendrosicus spathicalyx* has smaller leaves and

a spathaceous calyx; *D. kennedyi* has a much thinner, evenly bilabiate calyx with each lobe sharply apiculate; *D. isthmicus* has a thinner calyx and narrowly elliptic, usually smaller, leaves.

CHIRIQUÍ: Central valley of Río Chiriquí Viejo, *Allen 1362* (GH, MO, NY, US). Near Boquete, *Blum & Dwyer 2570* (MO, SCZ). Bajo Chorro, Boquete District, *Davidson 410* (MO). Cerro Horqueta NW of Boquete, *Dwyer et al. 444* (GH, MO, US); *Dwyer & Hayden 7694* (K, MO). Nueva Suissa, *Gentry 5982* (MO). 2 mi. E of El Hato del Volcán, *King 5305* (K, US). Around El Boquete, *Pittier 3001* (NY, US). Río Chiriquí Viejo valley near El Volcán, *White 227* (GH, MO, US).

5. **Dendrosicus spathicalyx** A. Gentry, Phytologia 26: 439. 1973. TYPE: Panama, *Gentry 5769* (MO, SCZ).—FIG. 11C–G.

Small, leaning *tree* 5–7 m tall, 15 cm d.b.h., the bark thickly moss-encrusted; the twigs decurrent below the nodes. *Leaves* alternate, narrowly elliptic to narrowly obovate-elliptic, acute to long acuminate, basally cuneate or attenuate, essentially sessile, the extreme base swollen and woody, conspicuously jointed at nodes, 7.5–16 cm long and 2.1–4.3 cm wide, chartaceous, the secondary nerves 6–12 on a side, slightly raised above, conspicuously so beneath, the veinlets minutely and intricately impressed above and beneath, the surface thus roughened and shagreened. *Inflorescence* a single flower borne from a bracteate short-shoot on an older twig, the pedicel glabrous, red when fresh. *Flowers* with the calyx membranaceous, 4–4.1 cm long and ca. 2 cm wide, spathaceously split adaxially to 0.8–1 cm from the base with a tendency to tardily circumcissile dehiscence, glabrous, light green when fresh; corolla cream to whitish basally, becoming greenish white toward the mouth, campanulate with a transverse fold in the throat, 5.5–5.8 cm long and 1.8–1.9 cm wide at the mouth, the tube 3.7–3.8 cm long, the lobes fused into a reflexed rim, 1.7 cm wide, glabrous with a glandular epidermis inside and out, becoming stalked glandular-lepidote distally outside; stamens subexserted, the anther thecae slightly divergent, 7–8 mm long and 1.5–2 mm wide, the anterior filaments 2.5–2.6 cm long, inserted 1.7–1.8 cm from the base of the tube, the posterior filaments 2.3–2.4 cm long, inserted 2.0–2.1 cm from the base of the tube, the staminode 1.1–1.2 cm long, inserted 1.0 cm from the base of the tube, bent straight out from the corolla; pistil (partially destroyed in all flowers examined) with the ovary rounded conical, 4 mm long and 3–4 mm wide, lepidote, the ovules widely spaced, irregularly 8-seriate on each of 2 projecting parietal placentae, the placentae almost meeting but fused only at the extreme base; disc annular-pulvinate, 2 mm long and 9 mm wide. *Fruit* a pepo or calabash, ellipsoidal, pointed.

This species is known only from the tropical wet forest on top of Cerro Campana. Its unique, thin, dorsally split, spathaceous calyx is distinctive. Its bracteate short-shoots relate it to *D. macrophyllus*, as does the intricately impressed finer venation of the leaves. Except for the calyx this species appears similar to *Dendrosicus silvicola* (L. O. Wms.) A. Gentry. An additional fruiting collection, *Kennedy & Foster 2147* from the Rio Guanche, Colon Province, may represent this species, but without buds or flowers I am unable to positively distinguish it from *D. isthmicus*.

PANAMÁ: Cerro Campana, *Croat 14765* (MO, SCZ); *Dressler 3943* (MO); *Gentry 5769* (MO, SCZ).

12. DISTICTELLA

Distictella O. Kuntze *in* Post & O. Kuntze, Lex. Gen. Phan. 182. 1903. LECTOTYPE: *D. mansoana* (DC.) Urb.

Distictis Bur., Mon. Bignon. 46. 1864, non Mart. *ex* Meisn.

Lianas, rarely shrubs, branchlets terete; stems with 4 phloem arms in cross section; branchlets terete without interpetiolar glandular fields; pseudostipules inconspicuous, short and thick. *Leaves* 3-foliolate, the terminal leaflet often replaced by a trifid tendril. *Inflorescence* a terminal or axillary raceme or racemose panicle. *Flowers* with the calyx cupular, truncate, thick, usually with glandular fields below the margin; corolla white, tubular-campanulate, densely short-pubescent outside; anthers glabrous, the thecae straight, divaricate; pollen grains ecolpate, the exine alveolate; ovary ovoid-oblong, puberulous, the ovules 4–8-seriate in each locule; disc annular-pulvinate. *Fruit* a compressed or biconvex oblong capsule, the valves parallel to the septum, thick and woody, smooth or minutely rough-surfaced, often shortly puberulous; seeds thin but usually more or less woody, the wings glabrous, usually brown, often more or less reduced.

About 10 species in continental tropical America ranging from Costa Rica to Brazil. The genus has not previously been reported in Central America.

Distictella magnoliifolia (H.B.K.) Sandw., Lilloa 3: 460. 1938.—FIG. 12.

Bignonia magnoliaefolia [*sic*] H.B.K., Nov. Gen. Sp. Pl. 3: 136. 1819. TYPE: Venezuela, Javita, *Humboldt & Bonpland 973* (P).
B. alliacea Lam. sec. Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 5. 1842, non Lam.
Distictis racemosa Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 179. 1897. SYNTYPES: Surinam, *Wullschlagel 1033* (BR); Brazil, Para, *Martius s.n.* (BR).
Bignonia rusbyi Britt. *ex* Rusby, Bull. Torrey Bot. Club 27: 71. 1900. TYPE: Bolivia, junction of Ríos Beni and Madre de Dios, *Rusby 1140* (NY).
Distictis kochii Pilg., Fedde Repert. 8: 151. 1910. TYPE: Brazil, Vaupes region, *Koch-Grunberg s.n.* (B-destroyed; K, photo).
Distictella broadwayana Urb., Fedde Repert. 14: 310. 1916. TYPE: Tobago, near Menna, *Broadway 4753* (BM).
D. kochii (Pilg.) Urb., Fedde Repert. 14: 310. 1916.
D. racemosa (Bur. & K. Schum.) Urb., Fedde Repert. 14: 310. 1916.

Liana to at least 7 cm in diameter, the bark somewhat fibrous, vertically striate, twisting to form a bush rope; stem with 4 phloem arms in cross section at least when young; branchlets terete, often somewhat flattened at the nodes, appressed-puberulous, usually reddish brown; nodes without interpetiolar glandular fields, the pseudostipules short and thick, inconspicuous. *Leaves* 2-foliolate with a tendril or tendril scar; leaflets more or less elliptic, acute to acuminate, the base widely cuneate, often briefly truncate at the apex of petiolule, 13.5–29 cm long and 6.1–13.0 cm wide, chartaceous to subcoriaceous, secondary veins 7–9 on each side, lepidote beneath and less so above, beneath appressed puberulous on the midvein and pubescent in axils of lateral nerves with some plate-shaped

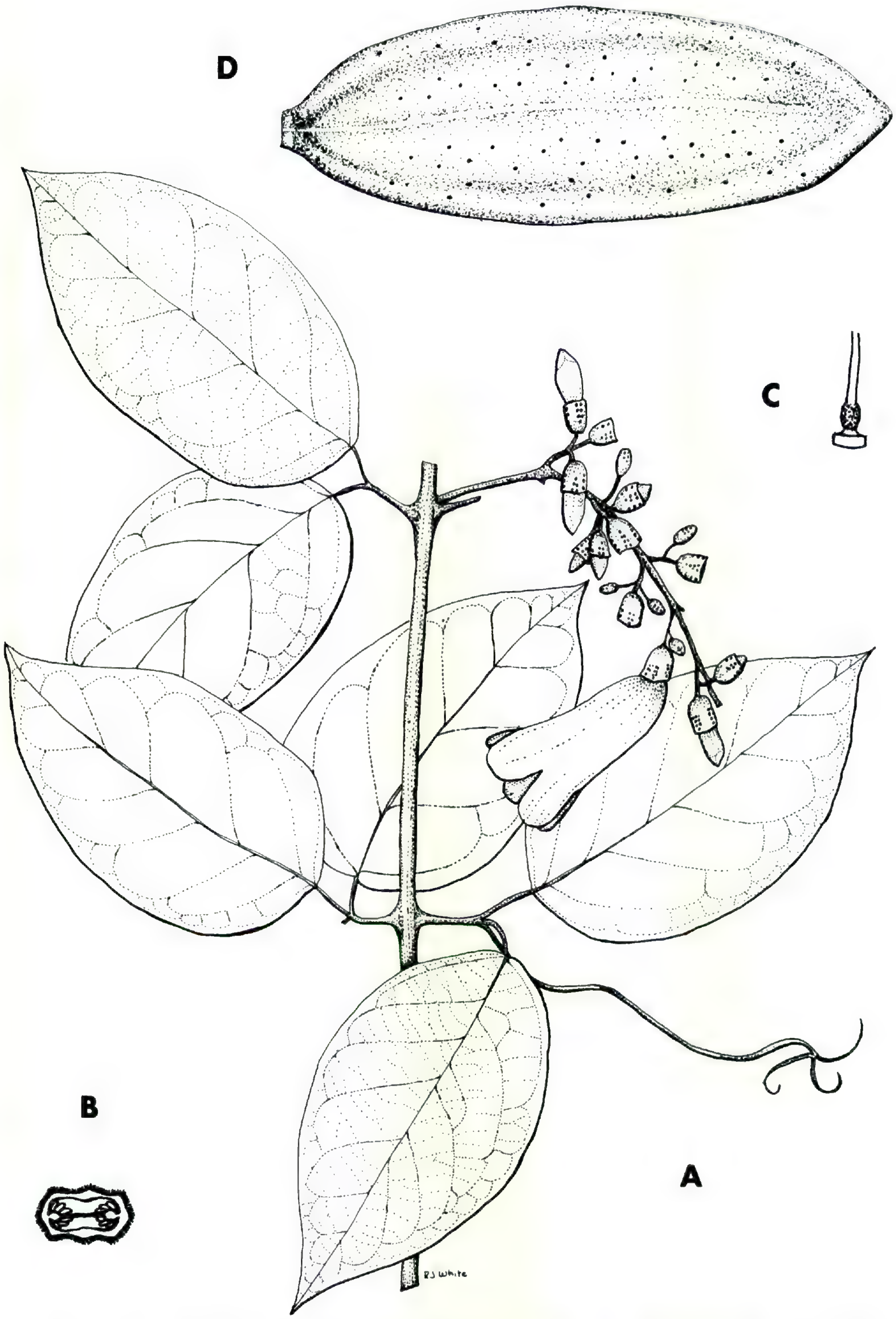


FIGURE 12. *Distictella magnoliifolia* (H.B.K.) Sandw.—A. Habit (× 3/5).—B. Ovary and disc (× 3/5).—C. Ovary cross section (× 7 1/5). [After *Woytkowski 5140*, Peru, and *Gentry 737* (both MO).]—D. Fruit (× 3/5). [After *Krukoff 6728*, Brazil (MO).]

glands near the midvein, sometimes also apically, above somewhat puberulous on the midvein, drying brownish-olive with the veins usually impressed; tendril trifid, 6–16 cm long to branching, the arms 0.2–1.5 cm long; petiolules and petiole appressed-puberulous and lepidote, prominently jointed, the petiolules 0.9–2.7 cm long, the petiole 1.8–5.8 cm long. *Inflorescence* a racemose panicle, its branches densely subpuberulous. *Flowers* with the calyx cupular, thick, subtruncate, 7–10 mm long and 6–8 mm wide, short-puberulous with linear fields of plate-shaped glands descending from the rim in the upper half; corolla white, thick, tubular-campanulate above a short, narrowed base, often bent slightly at the middle, 4.5–6.0 cm long and 1.4–1.7 cm wide at mouth, the tube 3.2–4.0 cm long, the lobes 1.0–1.2 cm long, densely short-pubescent on the tube outside and on the lobes, the tube glabrous inside except for dense glandular trichomes which form a ridge at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 4–5 mm long, the longer filaments 2.1–2.3 cm long, the shorter filaments 1.6–1.7 cm long, the staminode 6–8 mm long, inserted 7–10 mm from the corolla base; pistil 3.8–3.9 cm long, the style appressed-puberulent, the ovary flattened-ellipsoid, 3–4 mm long and 2 mm wide, 1.5 mm thick, densely appressed-puberulent, the ovules more or less 6-seriate in each locule; disc pulvinate with a narrowed neck, 1.5–2 mm long and ca. 4 mm wide. *Capsule* (*Krukoff 6728* (MO), Amazonas, Brazil) elliptic-oblong, somewhat compressed, the valves thick and woody, the midrib not visible, 10–15 cm long and 5–6 cm wide, 1.6–1.7 cm thick, appressed-tomentose with numerous, small, black-drying glandular areas, yellowish-brown in color as the trichomes, the surface somewhat roughened; seeds 2.1–2.4 cm long and 3.9–4.0 cm wide, flat and thin but brown and more or less woody.

A vine of the tropical wet forest, this species ranges from Costa Rica to Brazil. In the field the trifid tendrils and subterete, thick, smooth, reddish twigs, somewhat flattened at the nodes, identify it vegetatively.

The material referred to here has gone under the name *D. racemosa*, supposedly distinct from *D. magnoliifolia* on the basis of leaflets with veins and veinlets impressed above and lacking glandular fields. Both characters are variable, and the distinction does not seem adequate for specific separation.

The description of the fruit of this species is based on extra-limital material. All of the fruits I have seen on South American collections are quite homogeneous, according well with this description, but a single unattached capsule valve collected from the forest floor at Jaqué apparently belongs to *Distictella* and is notably different from the South American collections I have seen. This valve is glabrous except for dense lepidote scales and is reddish brown in color, although agreeing in size and shape. If this capsule valve is found to be representative of the Central American plant, then a re-examination of its taxonomic position is in order.

CANAL ZONE: Pipeline Road, TTC transect 3, *Gentry 7400* (MO). COLÓN: Santa Rita Ridge, *Croat 13183* (MO, SCZ); *Gentry 737, 1861, 1882B* (all MO). DARIÉN: S of Jaqué, *Gentry 4125* (MO). Slopes of Cerro Chucula, *Gentry 4265* (MO).

13. GODMANIA

Godmania Hemsl., Diag. Pl. Mex. Centr. Amer. 35. 1879. TYPE: *G. macrocarpa* (Benth.) Hemsl. = *G. aesculifolia* (H.B.K.) Standl.

Small to medium-sized *trees*. *Leaves* digitately 5–9-foliolate. *Inflorescence* a large terminal corymbose panicle. *Flowers* with the calyx small, less than 2 mm long, broadly campanulate, shortly 5-lobed; corolla yellow ventrally and orange-brown dorsally with edges of the lower 3 lobes also brownish, urceolate, bilabiate, less than 1.6 cm long, puberulous; anthers pubescent, the thecae divaricate, less than 1 mm long, the filaments pubescent; pollen grains single, 3-colpate, the exine microreticulate; ovary linear-conical, lepidote and more or less puberulent, the ovules multiseriate in each locule; disc pulvinate. *Fruit* a linear capsule, dehiscing perpendicularly to the septum; seeds bialate, with long, sharply demarcated, irregular-ended, hyaline-membranaceous wings.

One species of continental tropical America ranging from Mexico to Brazil and Bolivia.

Godmania aesculifolia (H.B.K.) Standl. *in* Standl. & Calderon, Lista Prelim. Pl. El Salvador 200. 1925.—FIG. 13.

Bignonia aesculifolia H.B.K., Nov. Gen. Sp. Pl. 3: 140. 1819. TYPE: Mexico, Guerrero, *Humboldt & Bonpland 3902* (P).
Tecoma digitata H.B.K., Nov. Gen. Sp. Pl. 3: 142. 1819. TYPE: Colombia, Santa Cruz, *Humboldt & Bonpland 321* (P).
T. fuscata Moc. *ex* DC., Prodr. 9: 218. 1845. TYPE: (not seen).
T.? aesculifolia (H.B.K.) DC., Prodr. 9: 221. 1845.
Cybistax macrocarpa Benth. *in* Benth. & Hook., Gen. Pl. 2: 1043. 1876. TYPE: Panama, near Panamá and Río Grande Station, *Hayes 61* (BM, K, P).
Godmania macrocarpa (Benth.) Hemsl., Diag. Pl. Mex. Centr. Amer. 2: 35. 1879.
Tabebuia aesculifolia (H.B.K.) Hemsl., Biol. Centr. Amer. Bot. 2: 494. 1882.
T. fuscata (Moc. *ex* DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 494. 1882.
Godmania uleana Kränzl., Notizbl. Bot. Gart. Berlin 6: 379. 1915. TYPE: Brazil, Rio Branco, *Ule 7696* (US).

Small to medium-sized *tree* to 13 m tall and 30 cm d.b.h; bark smooth to longitudinally ridged; twigs puberulous to subpuberulous, terete, thick with a large pith, foul-smelling when broken (as the inner bark) with an odor reminiscent of horse urine. *Leaves* digitately (5–)7–9-foliolate; the leaflets more or less obovate or oblanceolate, acute, attenuate-cuneate, membranaceous, secondary veins 7–13 on a side, above and beneath simple puberulous especially along veins, densely impressed-lepidote, usually with a few plate-shaped glands along the midvein beneath, drying more or less olive above and brownish beneath, the terminal leaflet 8.2–16.5 cm long and 3.1–7.2 cm wide, the first intermediate pair 6.7–17.5 cm long and 2.5–7.0 cm wide, the second pair 5–15.2 cm long and 2–5.6 cm wide, the third pair 2.7–6.5 cm long and 0.9–2.9 cm wide, the fourth pair when present smaller, the terminal to basal petiolules 0.2–2.3 cm, 0.2–1.6 cm, 0.2–0.9 cm, and 0.2–0.7 cm long respectively; petiole 6.6–15.5 cm long, puberulous as the petiolules. *Inflorescence* a flat-topped, terminal panicle of few to many flowers, its branches puberulous. *Flowers* with a musky odor, only a few opening

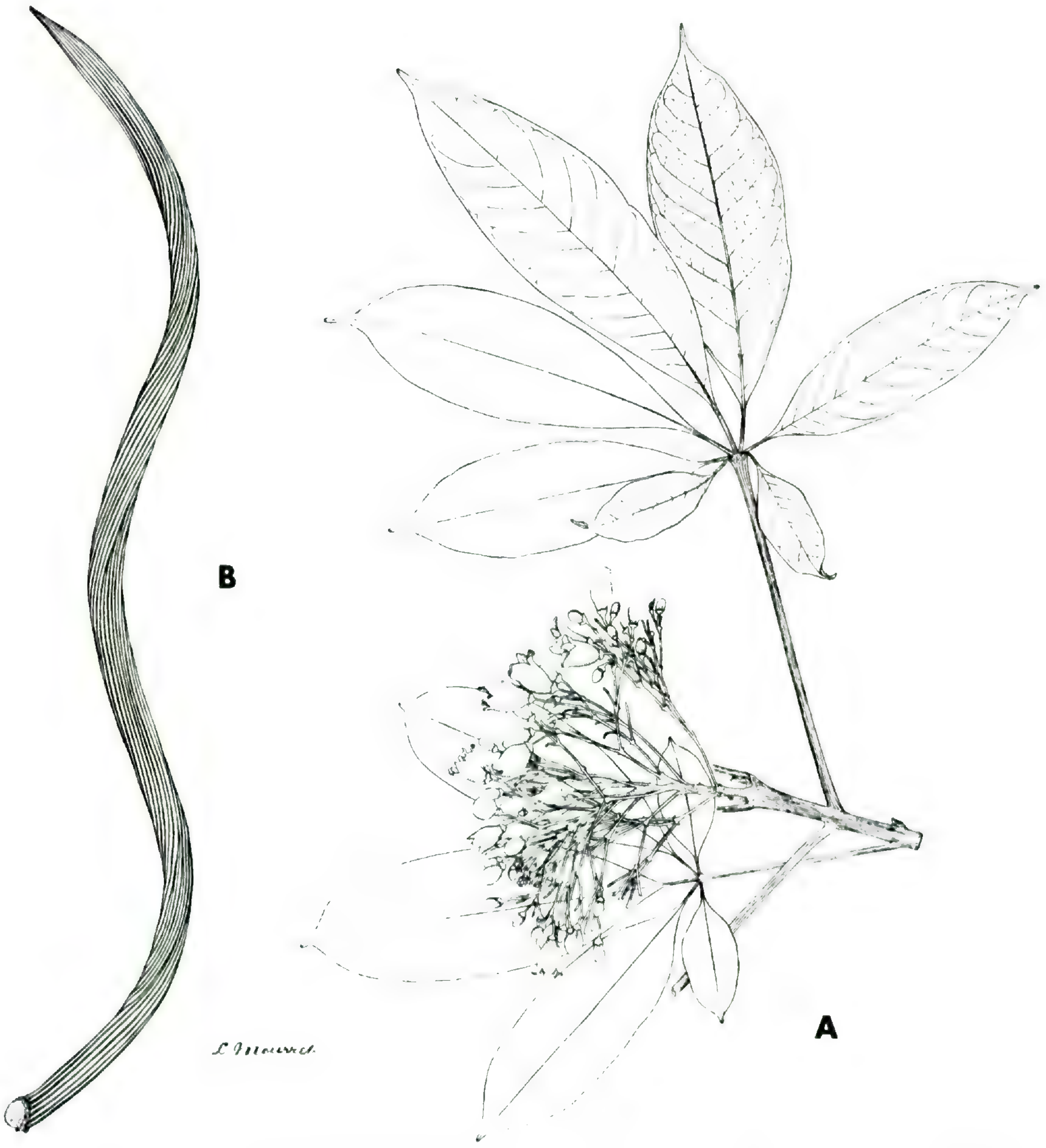


Figure 13. *Godmania aesculifolia* (H.B.K.) Standl.—A. Habit (× ½). [After *Allen 4492* (MO).]—B. Fruit (× ¼). [After *Gentry 359*, Costa Rica (MO).]

at a time; calyx widely campanulate, shortly 5-lobed, lepidote and simple-puberulent, 1–2 mm long and 2–4 mm wide; corolla yellow ventrally and orangish-brown dorsally outside, inside the ventral throat and most of the lower 3 lobes yellow, the dorsal 2 lobes brownish at the edges of the lower 3 lobes and the dorsal part of the throat, urceolate, 1.0–1.6 cm long and 7–8 mm wide, the tube 9–10 mm long, the upper 2 lobes 0.2–0.3 cm long, the 3 lower lobes 0.4–0.3 cm long, simple-puberulent outside, short-pubescent inside on the edges of the lobes with long, simple trichomes on the lower lobe, in the floor of throat, and sparsely at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, pubescent, less than 1 mm long, the filaments pubescent, the longer pair 0.8–1.0

cm long, the shorter pair 0.6–0.7 cm long, the staminode 0.4 cm long, inserted 1–3 mm from base of corolla tube; pistil curved to fit against the corolla roof, 1.1 cm long, the ovary linear-conical, 2 mm long, 1 mm wide, strongly lepidote and somewhat simple-puberulous, the ovules multiseriate; disc pulvinate, inconspicuous, 0.5 mm long and 1.5 mm wide. *Capsule* linear, corkscrew-twisted, 45–100 cm long and 0.9–1.5 cm wide, terete, longitudinally finely ridged, somewhat simple-puberulous; seeds thin, bialate, 0.9–1.5 cm long and 7.0–13.5 cm wide, the wings hyaline-membranaceous, sharply demarcated, narrow, long, irregular-ended.

A tree of the tropical dry forest and premontane moist forest, this species also occurs less commonly in drier parts of the tropical moist forest. It ranges from Mexico to Brazil and Bolivia. It flowers primarily in the dry season, and fruit set is in middle or late dry season.

The tiny flowers (less than 1.6 cm) are the smallest of the neotropical Tecomeae and are distinctive in shape and color pattern. The spirally twisted fruit is unique among mainland Bignoniaceae (*Spirotecoma* of the West Indies has a similar fruit). The leaves vary extensively in shape and amount of pubescence, but the attenuate more or less apetiolular leaflet base is a fairly constant distinguishing character. Another field character, especially useful when the tree is leafless, is the rank odor of the broken twigs.

CANAL ZONE: Vicinity of Summit, *Allen 4492* (GH, MO, P, U, US). Near beach at Fort Kobbe, *Duke 4244* (K, MO). NE of Summit, *Fosberg 27394* (NY). W end of Thatcher Ferry Bridge, *Gentry 1394* (MO). Pipeline Road, *Gentry 2096* (MO). Near City of Panamá, *Hayes 61* (BM). Near Gamboa, *Pittier 3703* (GH, NY, US). Las Sabanas, *Pittier 6720* (C, NY). *Pittier 7002* (US). Near Balboa, *Standley 29238, 32130* (both US). Chiva Chiva Trail, *Tyson 1335* (MO, SCZ). Albrook Air Force Base, *Tyson 2041* (SCZ). Chiva Chiva Trail, *Tyson & Blum 3569* (GH, MO, SCZ). Curundu, *Tyson & Dwyer 4456* (GH, MO, NY, SCZ, US). Near bridge between "our" island and mainland, *White 105* (GH, MO, US). CHIRIQUÍ: Vicinity of Boquete, *Allen 1018* (MO). W of Río Chorchita, *Gentry 5851* (MO). DARIÉN: *Sexton 116* (MO). HERRERA: La Cabuya, Las Minas, *Lao 140* (MO). PANAMÁ: Below El Valle, *Gentry & Dwyer 3675* (MO). Near Panamá, *Hayes 61* (BM, K, P). Pedregal, Ciudad de Panamá, *Holdridge 6505* (MO, PMA). N of Panamá City, *Paul 455* (US). Juan Díaz, *Standley 30594* (US). Río Tapia, *Standley 30678* (US). Nuevo San Francisco, *Standley 30699* (US). Between Las Sabanas and Matías Hernández, *Standley 31816, 31845* (both US). VERAGUAS: NE of La Mesa, *Blum & Tyson 654* (MO, SCZ). WITHOUT LOCALITY: *Duchaissing s.n.* (GH); *Grisebach s.n.* (MO).

14. HAPLOPHRAGMA

Haplophragma Dop, Bull. Soc. Bot. France 72: 889. 1925. TYPE: *H. adenophyllum* (Wall. *ex* G. Don) Dop.

Trees. *Leaves* imparipinnate, glabrous to tomentose. *Inflorescence* an axillary or terminal, many-flowered panicle. *Flowers* with the calyx campanulate or tubular-campanulate, irregularly 2–5-lobed; corolla broadly campanulate above a tubular base, pubescent outside; anthers slightly divergent, gabrous or puberulous; ovary cylindrical, pubescent, the ovules multiseriate in each locule; disc annular-pulvinate. *Fruit* a cylindrical capsule, more or less terete, usually spirally twisted, dehiscent perpendicular to the septum; seeds flat, winged.

Two species native to southeast Asia.

1. **Haplophragma adenophyllum** (Wall. *ex* G. Don) Dop, Bull. Soc. Bot. France 72: 890. 1925.—FIG. 14.

Bignonia adenophylla Wall., Cat. 6502. 1832, nomen nudum.
B. adenophylla Wall. *ex* G. Don, Gen. Syst. 4: 221. 1838. TYPE: (not seen).
Spathodea adenophylla (Wall. *ex* G. Don) DC., Prodr. 9: 206. 1845.
Heterophragma adenophyllum (Wall. *ex* G. Don) Seem. *ex* Benth. & Hook., Gen. Pl. 2: 1047. 1875.

Tree 10 m tall, 25 cm d.b.h.; branchlets thick, terete. *Leaves* pinnately compound (3–)5–7-foliolate, the upper leaflets 14–21 cm long and 9–13 cm wide, the lowest leaflet pair near the base of petiole, much reduced, resembling foliaceous pseudostipules, all leaflets elliptic to elliptic-ovate, obtuse, basally truncate, stellate pubescent with mostly few-armed trichomes, especially beneath. *Inflorescence* an open panicle, its branches pubescent with brown stellate trichomes. *Flowers* with the calyx cupular-campanulate, irregularly 3–5-lobed, 3.7–5 cm long and 2.5–3.7 cm wide, densely pubescent with brown stellate trichomes, these interspersed with longer, pale, fimbriate-stellate trichomes; corolla light yellow, the tube brown outside from the pubescence, broadly campanulate above a 1.2–1.4-cm-wide neck, the extreme base enlarged to 2–2.5 cm, 8–9 cm long and 4–4.5 cm wide at mouth, the tube 6–7 cm long, the lobes 2–3 cm long; stamens subexserted, the thecae parallel or slightly divergent, 6–7 mm long, slightly pubescent near attachment to connective, the posterior filaments 3.8–4.1 cm long, the anterior filaments 4.6–4.8 cm long, the staminode 14–15 mm long, inserted 2.2–2.5 cm from the base of tube; pistil 6.5–7.1 cm long, the style base stellate pubescent; ovary cylindrical, 6–9 mm long and 4–5 mm wide, densely brown-pubescent with stellate trichomes, the ovules multiseriate; disc annular-pulvinate, 3–4 mm long and 14–15 mm wide. *Capsule* linear, terete with 8 slightly raised, longitudinal ridges, spirally twisted, 55–100 cm long and 1.5–2 cm wide, conspicuously stellate-pubescent with brown trichomes, spotted with small, lighter, glabrous lenticels, the calyx persistent; seeds flat, 0.8–1.1 cm long and 3.4–3.7 cm wide, the wings hyaline-membranaceous.

A species of southeast Asia ranging from Burma to Malaysia, *H. adenophyllum* is cultivated occasionally elsewhere in the tropics. Two trees of this species are cultivated at Summit Gardens.

CANAL ZONE: Summit Gardens, *Gentry 1446A* (MO, SCZ).

15. JACARANDA

Jacaranda Juss., Gen. Pl. 138. 1789. TYPE: *J. caerulea* (L.) St. Hilaire.

Iacaranda Persoon, Syn. Mant. 2: 173. 1805, sphalma.
Kordelestris Arruda *in* Koster, Trav. Braz. 1: 500. 1816, fide *Index Kewensis*.
Rafinesquia Raf., Sylva Tell. 79. 1838, non Nutt. TYPE: *R. caerulea* (L.) Raf. = *Jacaranda caerulea* (L.) St. Hilaire.
Etorloba Raf., Sylva Tell. 79. 1838, nom. alt. for *Rafinesquia*: "another beautiful G. that I dedicate to myself if the *Rafinesquia* of New Flora 600 is not deemed good enough, and I add a second name meaning 'heart pod,' if any one cavils at this again."—Rafinesque.
Pteropodium DC. *ex* Meissn., Gen. 300; Comm. 209. 1840. LECTOTYPE: *P. glabrum* DC. = *Jacaranda glabra* (DC.) Bur. & K. Schum.

FIGURE 14. *Haplophragma adenophyllum* (Wall. *ex* D. Don) Dop.—A. Habit (× ¼). —B. Fruit (× ¼). [After *Gentry 1446A* (MO).]

Mostly medium-sized to large *trees* (some Brazilian species are shrubs or subshrubs). *Leaves* usually bipinnate (rarely pinnate or even simple in some Brazilian species). *Inflorescence* a few- to many-flowered terminal or axillary panicle, sometimes from the old wood. *Flowers* with the calyx short and broadly campanulate to cupular, more or less truncate, usually 5-denticulate or acutely 5-lobed; corolla blue or blue-purple tubular-campanulate, pubescent to essentially glabrous outside; anthers glabrous, often 1-thecate, the staminode elongate, ex-

ceeding the stamens, variously glandular-pubescent especially at the tip; pollen grains 3-colpate, the exine smooth; ovary flattened-cylindrical, glabrous or pubescent (even in the same species), the ovules ca. 8-seriate in each locule; disc pulvinate. *Fruit* an oblong capsule strongly flattened perpendicularly to the septum, dehiscing perpendicularly to the septum and parallel to the plane of compression, the valves variously glabrous or lepidote, often with undulate margins; seeds thin, winged, the wings membranaceous, hyaline or brownish.

About 30 species of tropical America ranging from southern Mexico and the West Indies to Argentina, widely cultivated in the Old World. Opposite bicompound leaves distinguish most species of *Jacaranda* from other New World trees of the Bignoniaceae.

Useful reference:

Dugand, A. Sobre *Jacaranda* (Bignoniaceae) de Colombia y Venezuela. Mutisia 23: 1–16. 1954.

a. Corolla tube densely puberulous outside; fruit drying black or brown without freckling of paler spots, the margin not undulate.
  b. Calyx tubular-cupular; inflorescence a racemose panicle; fruit oblong; leaflets large (more than 1.5 cm long and 0.8 cm wide); native, rarely cultivated ..... 2. *J. copaia*
  bb. Calyx short, broadly campanulate; inflorescence an open panicle; fruit suborbicular; leaflets small (less than 1.2 cm long and 0.4 cm wide); cultivated exotic, mostly at higher elevations ..... 3. *J. mimosifolia*
aa. Corolla tube glabrate outside, glandular pubescent at the base; fruit drying blackish with a freckling of tan or whitish spots, the margin more or less undulate at maturity ..... 1. *J. caucana*

1. **Jacaranda caucana** Pittier, Contr. U.S. Natl. Herb. 18: 258. 1917. TYPE: Colombia, Cauca, *Pittier 925* (US).

J. filicifolia D. Don sec. Seem., Bot. Voy. Herald 181. 1854, non Don.
J. gualanday Cortes, Fl. Col. 99. 1897, nomen nudum.
J. trianae Kränzl., Fedde Repert. 17: 226. 1921. TYPE: Colombia, Cundinamarca, *Triana s.n.* (G).

1a. **Jacaranda caucana** Pittier subsp. **sandwithiana** A. Gentry.[5] TYPE: Panama, Canal Zone; cultivated at Summit Gardens, *Gentry 744* (MO).—FIG. 15.

Tree to at least 39 cm d.b.h. and 25 m tall; the trunk usually somewhat flattened, bark light gray, smooth; twigs lepidote, subterete, gray with somewhat elongate whitish lenticels. *Leaves* pinnately bicompound, 24–43 cm long, with 8–18 pinnae, each pinna 10–13.2 cm long with winged rachis and 11–23 sessile leaflets, these 0.8–3.0 cm long and 0.4–1.0 cm wide, in the shape of a parallelogram with the midvein connecting the 2 acute angles except the rhombic terminal one, 3–3.5 cm long and 1.3–1.8 cm wide, apically obtuse and apiculate, basally abruptly wide-cuneate, membranaceous, secondary veins in 4–7 pairs, lepidote above and beneath, pubescent beneath especially along the veins with long simple trichomes and sparsely above with short simple trichomes, drying brownish-green

[5] *Jacaranda caucana* Pittier subsp. *sandwithiana* A. Gentry, subsp. nov. Ab subspecie typica foliolis majusibus, pinnis plus separatis, lobis calycis abbreviatis differt.

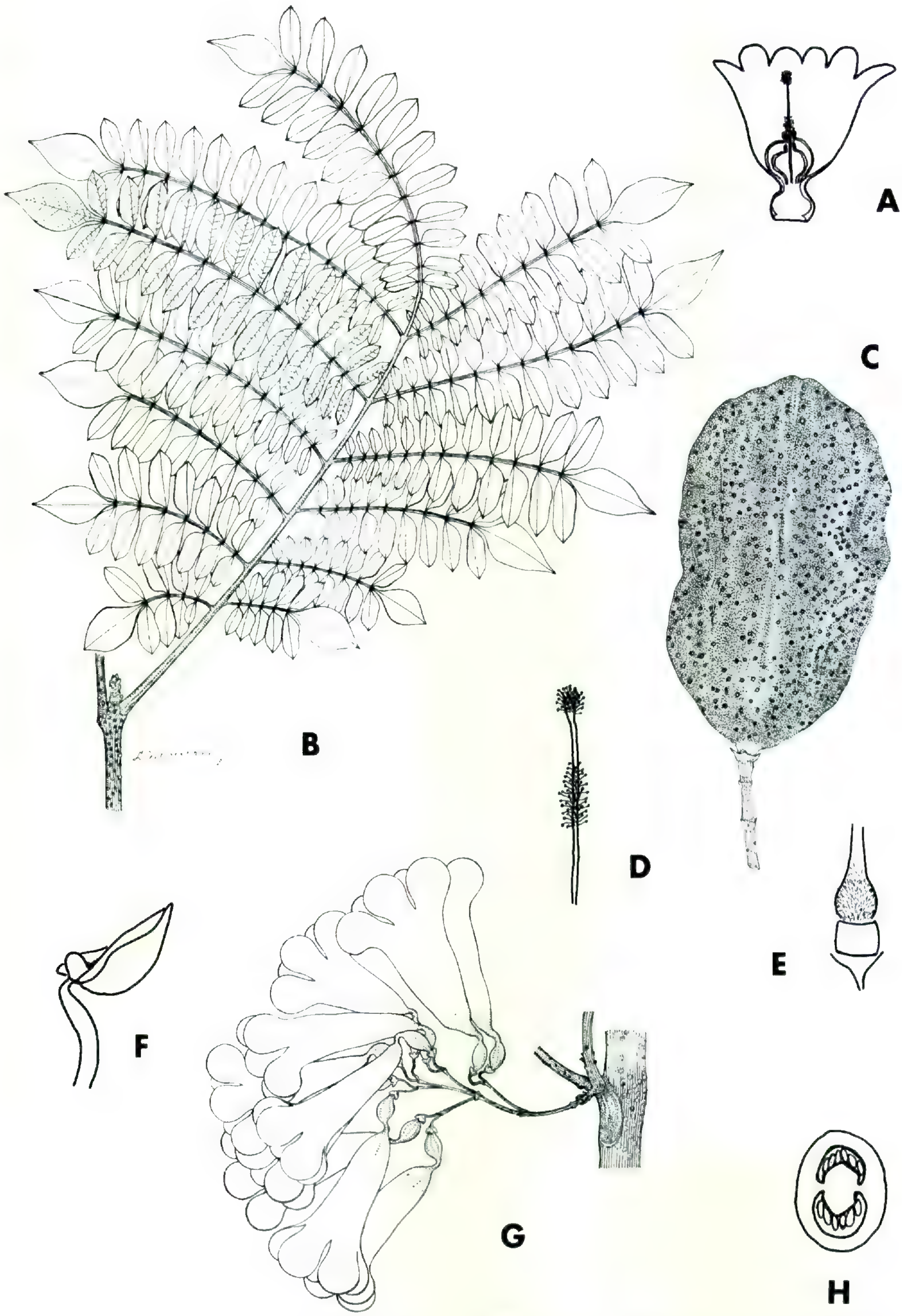


FIGURE 15. *Jacaranda caucana* subsp. *sandwithiana* A. Gentry.—A. Corolla slit open (× 3/5).—B. Leaf (× 3/5).—C. Fruit (× 3/5). [After *Gentry 1939* (MO).]—D. Staminode (× 1 4/5).—E. Ovary and disc (× 4 1/5).—F. Anther (× 12).—G. Inflorescence (× 3/5).—H. Ovary cross section (× 7 4/5). [After *Gentry 744* (MO).]

above, grayish beneath; petiole 4.5–7 cm long, the petiolules 4–10 mm long, petiole and petiolules lepidote and sparsely simple pubescent as the main and lateral rachises. *Inflorescence* a cluster of 3–27-flowered panicles on older twigs, the pedicels and peduncle simple-puberulous. *Flowers* with a delicate sweet fragrance; calyx reduced, broadly campanulate, subtruncate to bluntly 5-toothed, simple-puberulous and scattered-lepidote, 1.5–3 mm long and 3–4 mm wide; corolla purplish-blue outside and on the lobes and abaxially on throat inside, white at base of throat inside and adaxially to the base of the 2 adaxial lobes, tubular-campanulate above a 5–9 mm × 5–7 mm basal bulge and 3–4 mm × 1.2 mm neck which bends 90°, 3.6–4.8 cm long and 1.1–2.0 cm wide at the mouth, the tube 3.0–3.6 cm long, the lobes 0.7–1.0 cm long; the tube mostly glabrous outside, glandular-puberulous on the neck, the adaxial lobes and tube densely minute-lepidote inside, the tube also with a few long simple trichomes in the throat and glandular-puberulous with 1–3-celled trichomes at the level of stamen insertion and in the neck, the abaxial lobe pubescent inside with long, simple or forked trichomes, the others often ciliate; stamens didynamous, the anthers 1-thecate, 1.5–2 mm long, the anterior filaments 1.2–1.5 cm long, the posterior filaments 1.1–1.4 cm long, inserted 8–15 mm from the base of tube; the staminode 2.2–2.5 cm long, glandular-pubescent with long (to 2 mm) 1–6-celled trichomes for the apical 2–3 mm and central 5–7 mm; pistil 2.0–2.6 cm long, bent to follow the posterior contour of the corolla, the ovary flattened-cylindrical, 1.5–2 mm long and 1.5–2 mm wide, 1–1.5 mm thick, appressed-pubescent with simple unicellular trichomes, the ovules 4–6-seriate in each locule; disc pulvinate, 1–1.5 mm long, 1–2 mm wide. *Capsule* compressed-oblong with undulate margins at maturity, 4.6–8.5 cm long and 3.8–6.0 cm wide, lepidote, drying dark with slightly raised lighter spots; seeds 0.8–1.6 cm long and 2.3–4.1 cm wide, the wings brown to subhyaline, the body slightly thicker and relatively woody, not distinctly demarcated.

In Panama this species has been collected only on the Pacific slope, mostly in the tropical moist forest. It is widely cultivated in the lowlands and its natural range is much obscured. The species is apparently disjunct across most of Panama between Darién and Chiriquí Provinces. It flowers in the dry season with an extended flowering period lasting more than a month. The fruit takes just over a year to mature, and seed release is usually in late dry season.

Jacaranda caucana ranges from southeastern Costa Rica to the valleys of the Río Cauca and Río Magdalena in Columbia. Its close relative, *J. hesperia* Dugand, occurs along the Pacific lowlands of Colombia in the departments of Valle and Choco and northward in the Atrato Valley into Antioquia Province south of Turbo.

On the basis of the Colombian material alone, the separation between *J. hesperia* and *J. caucana* is easily justified. Some of the most important differences by which *J. hesperia* is separated from *J. caucana* include larger leaflets and more widely separated pinnae, much larger fruits with straight margins, reduction of the glandular pubescence at the corolla base to glandular-lepidote scales, and a

different ecology. The Panamanian material is intermediate between the two Colombian species. It has the smaller, undulate-margined fruits with light spotting and the glandular pubescent corolla tube of *J. caucana* but the larger leaflets and widely spaced pinnae of *J. hesperia*. The Panamanian plants also differ notably from both *J. caucana* and *J. hesperia* in the short-lobed, sometimes subtruncate calyx.

All but one of the Panamanian and Costa Rican specimens come from areas of tropical moist forest, the single exception being from a transitional area at Caldera, Chiriquí. Thus the Darién plants represent not a continuation of the range of *J. hesperia* but a distinct population separated by the wet forest area near the Colombian border. While the habitat of *J. hesperia* is different from that of *J. caucana* as it occurs in Central America, the valleys of the Magdalena and Cauca Rivers in which typical *J. caucana* occurs are quite dry in places despite their greater elevation. Thus the Central American plants agree with typical *J. caucana* in everything but their leaves and calyces.

If variations in leaf dimensions are considered not to merit specific distinction, then only shorter calyx lobes remain to differentiate the Central American plants from *J. caucana*. There is sufficient variation in calyx lobe length, especially in specimens from the Darién, that I would consider this character, too, unworthy of specific recognition. The Panamanian plant should rather be regarded as a distinctive subspecies of *J. caucana* differentiated by its shorter calyx lobes and larger leaflets. I have named this variety for the late N. Y. Sandwith in recognition of his early understanding of its correct relationship. This is clearly documented by the correspondence between Sandwith and Dugand, which is filed in the herbarium at Kew. It is evident from this correspondence that Sandwith, though accepting *J. hesperia*, recognized the difficulty of assigning the Central American plants to it. In a marginal note next to Dugand's discussion of differences in fruit size he reminded himself to check the Sutton Hayes specimen in the carpological collection at Kew. After doing this he added in a second note that the Hayes fruit matched *J. caucana* rather than *J. hesperia*. Although Sandwith had access to only a few Central American collections he clearly understood the problem and his use of "*Jacaranda* aff. *caucana*" in identifying such material further underscores his grasp of the situation, although he failed to give the Central American plants formal taxonomic recognition.

CANAL ZONE: Summit Garden, *Croat 11201* (MO); *Gentry 1939* (MO, SCZ), *3691*, *4961* (both MO). Near Paraíso Station, Panama Railroad, *Hayes 12* (BM, BR, K). Fort Clayton, *Tyson 3463* (SCZ). Vicinity of Miraflores Locks, *White & White 190* (GH, US). CHIRIQUÍ: Quebrada Quanabanito W of Puerto Armuelles, *Croat 22080* (MO). Quebrada Melliza, Burica Peninsula, *Liesner 473* (MO). Caldera (Boquete) near banks of Río Chiriquí Viejo, *Maurice 866* (US). Vicinity of San Lorenzo, *Seemann 1127* (BM, K). DARIÉN: Río Chico, *Allen 4596* (MO). Cerro Piriaque, *Duke 8129* (MO). Río Tuira between Ríos Paya and Pucro, *Duke & Kirkbride 14055* (MO, SCZ). Isla Cartagena near La Palma, *Gentry 3934* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4411* (MO). Below Boca de Cupe on Río Tuira, *Gentry 4487* (MO). El Real, *Gentry 4531* (MO). Río Tuira between Sumacate and Chepigana, *Pittier 6622* (US). Vicinity of El Real, *Stern et al. 743* (GH, K, US). Cerro Piriaque, *Tyson et al. 3847* (MO). PANAMÁ: Vicinity of Arraiján, *Allen 1763* (F, GH, NY, US). Along highway between Chorrera and Bejuco, *Croat 14413A* (MO).

2. **Jacaranda copaia** (Aubl.) D. Don, Edinburg Phil. Jour. 9: 267. 1823.

Bignonia copaia Aubl., Hist. Pl. Guiane Fr. 2: 650, *tab. 262, fig. 1, tab. 265.* 1775. TYPE: French Guiana, *Aublet s.n.* (P-AD, 12304).
B. procera Willd., Sp. Pl. 3: 307. 1801. TYPE: Based on *B. copaia* Aubl.
Jacaranda procera (Willd.) R. Br., Bot. Mag. *tab.* 2327. 1822.
J. spectabilis Mart. *ex* DC., Prodr. 9: 229. 1845. TYPE: Brazil, Amazonas, *Martius*, 1819 (M).
J. superba Pittier, Bol. Soc. Venez. Ci. Nat. 6: 19. 1940. TYPE: Venezuela, Bolivar, *Llewelyn Williams 11537* (US).

Tree to 45 cm d.b.h. and 45 m tall, the trunk usually unbranched for most of its length and often somewhat flattened, young trees unbranched with a cluster of giant leaves at top, bark gray, smooth; twigs lepidote, subtetragonal, drying brown or blackish, the pith large, sometimes hollowed by ants. *Leaves* pinnately bicompound, 15–165 cm long, with 5–20 pinnae, each pinna 5–35 cm long with essentially wingless rachis and 5–25 sessile leaflets, these 1.5–8 cm long and 0.8–2.5 cm wide, asymmetrically rhombic-elliptic, acute to acuminate, asymmetrically attenuate, membranaceous, secondary veins 3–5 on one side and 4–6 on the other, lepidote with scabrous to puberulous midvein above and beneath; drying dark brown above, olive beneath, petiole 3.5–29 cm long, the petiolules 2.5–4 cm long, petiole and petiolules lepidote to subpuberulous as on the main and lateral rachises. *Inflorescence* a narrow terminal panicle, its branches lepidote and subpuberulous to puberulous. *Flowers* with the calyx cupular, more or less truncate with 5 subequal teeth, pubescent with simple or branched trichomes, 5–7 mm long and 3–5 mm wide, eglandular; corolla purplish-blue outside and on the lobes and abaxially on the throat inside, white adaxially on the throat inside and at the base of 2 adaxial lobes, tubular-campanulate above a 7–10 mm × 3–4 mm basal constriction, 3.2–5.0 cm long and 0.8–1.9 cm wide at the mouth, the tube 2.3–3.7 cm long, the lobes 0.3–1.4 mm long, densely puberulent outside with simple, forked, and mostly short dendroid trichomes, the lobes dendroid pubescent inside, the tube glabrous adaxially and pubescent with mostly simple or forked trichomes abaxially, pubescent with gland-tipped trichomes at the level of stamen insertion; stamens didynamous, the anthers 1-thecate, 1.5–2.0 mm long, the anterior filaments 1.1–1.3 cm long, the posterior filaments 0.8–1.0 cm long, inserted 7–10 mm from the base of the tube, the staminode 2.4–2.7 cm long, bifurcate at the tip, glandular-pubescent with long simple trichomes on the tip and central portion; pistil 1.5–1.8 cm long, the ovary flattened-cylindrical, 2–2.5 mm long and 2–2.5 mm wide, 1.5 mm thick, glabrous, the ovules more or less 8-seriate in each locule; disc pulvinate, 1 mm long and 2.5 mm wide. *Capsule* compressed-oblong, the margins straight, not wavy, 6.2–12.7 cm long and 3.3–6.0 cm wide, somewhat lepidote to glabrous, drying brown or blackish; seeds small-bodied with a surrounding suborbicular wing, 1.0–2.0 cm long and 1.7–2.8 cm wide, the body 3–5 mm long and 3–4 mm wide, the wing hyaline-membranaceous, with radial brownish striations, clearly demarcated from the seed body.

This is a widespread tree of the tropical moist forest, premontane wet forest, and tropical wet forest. It ranges from British Honduras to Brazil, Peru, and the Guianas. It flowers during the dry season from February to April, and seed release is in mid wet season in late July and early August. Juvenile trees are

extremely abundant in second growth situations and are one of the characteristic elements of wet forest second growth. Their terminal tuft of leaves on a long slender stem (a habit shared with juveniles of *Schizolobium parahybum* (Vell.) Blake, which are common in the same associations) provides part of the typical physiognomy of young second growth. In mature forest young trees survive only in tree-fall clearings, although seedlings sprout under the forest canopy.

The cupular calyx of this species distinguishes it from the other Central American species of *Jacaranda*. Its larger leaflets also distinguish it vegetatively from *J. caucana* and the cultivated *J. mimosifolia*.

BOCAS DEL TORO: Region of Almirante, *Cooper s.n.* (F). CANAL ZONE: Barro Colorado Island, *Croat 6782* (MO, NY, SCZ), *7888* (MO, SCZ), *10187*, *10820*, *11331*, *12196*, *15585*, *16211A*, *16518A* (all MO); *Foster 1429* (MO, PMA); *Gentry 425* (MO, WIS); *Kenoyer 525* (US); *Shattuck 197* (A, MO), *672*, *781* (both MO); *Standley 41025* (US); *Wetmore & Abbe 104* (A, GH, MO); *Zetek 5085* (MO). Near Pedro Miguel, *Allen 729* (A, GH, MO, US), *4465* (NY), *4466* (GH, U). Vicinity of Madden Dam, *Allen 4467* (K, MO). Monte Lirio, *Christopherson 121* (NY, US). Las Cruces trail in Madden Forest, *Gentry 1377* (MO), *1957* (MO, SCZ). Pipeline Road, *Gentry 1798* (MO). Paraíso Station, Panama Railroad, *Hayes 627* (BM, BR, K). Summit, *Higgins 309* (US). N of Frijoles, *Standley 27513* (US). COLÓN: Santa Rita Ridge, *Gentry 1867* (MO). DARIÉN: Vicinity of Pinogana, *Allen 4431* (K, MO, US). Near Santa Fé, *Duke 12281* (MO). S of La Palma, *Gentry 4294* (MO). Near Cerro Pirre on Río Parasenico, *Gentry 4717* (MO). Piriaque at River Lara, *Tyson et al. 4759*, *4768* (both SCZ). PANAMÁ: Vicinity of National Airport E of Panama City, *Allen 4460* (BM, BR, MO). Cerro Campana, *Gentry 1828* (MO). Cerro Jefe, *Gentry 2105* (MO). Río Maestra, *Gentry 2217*, *2218* (both MO). Río Pasiga, *Gentry 2255*, *2269* (both MO). Río Agua Clara, *Gentry 2603* (MO). Along trail between Río Espavé and Río Bayano, *Gentry 7752* (MO). 10–15 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3820* (MO). Between Río Sulugandí and Río Espavé, *Gentry 4982* (MO). W of El Llano on road to Cartí, *Gentry 5089* (MO). San José Island, *Johnston 635* (GH). SAN BLAS: Perme, *Cooper 631* (BM, K, NY, US). Mountains above Puerto Obaldía, *Gentry 1490* (MO). Mainland opposite Playón Chico, *Gentry 6370* (MO).

3. **Jacaranda mimosifolia** D. Don, Bot. Reg. *Tab. 631*. 1822. TYPE: (not seen).

J. ovalifolia R. Br., Bot. Mag. *tab. 2327*. 1822. TYPE: (not seen).
J. chelonia Griseb., Pl. Lorentz. 175. 1874, non Symb. Fl. Argent. 258. 1879. TYPE: (not seen).

Tree to at least 15 m tall and 45 cm d.b.h., the bark gray; branchlets terete. *Leaves* pinnately bicompound, 15–30 cm long, with 13–31 pinnae, these 1.3–2.1 cm apart on the rachis, each pinna 5–10 cm long with winged rachis and 13–41 sessile leaflets, these 3–12 mm long and 1–4 mm wide, narrowly elliptic, sharply acuminate, the base cuneate, chartaceous, glabrous or slightly puberulous along midrib and margin, the margin slightly revolute. *Inflorescence* an open terminal panicle, the branches shortly puberulous. *Flowers* with the calyx reduced, broadly campanulate, 5-denticulate, 1 mm long and 1.5–2 mm wide, subpuberulous at least along margin; corolla purplish-blue with the tube white inside, tubular-campanulate above a slightly narrowed neck which is inconspicuously curved and slightly enlarged toward the base, 3–4 cm long and 0.7–1.2 cm wide at the mouth of tube, the tube 2.4–5.2 cm long, the lobes 0.3–0.5 cm long pubescent outside, especially toward the base, pubescent inside at the level of stamen insertion and sparsely so with long trichomes in the tube; stamens didynamous, the anthers 1-thecate, the second theca reduced to a minute appendage, each theca 2 mm long, the anterior filaments 1.4–1.8 cm long, the posterior filaments

1.1–1.4 cm long, the filaments pubescent below the middle, inserted 1.1–1.2 cm from the base of tube, the staminode 2.0–2.5 cm long, the middle portion and tip glandular-pubescent, inserted 0.9–1.0 cm from the base of the tube; pistil 2.2–2.5 cm long, the ovary flattened-cylindrical 3–3.5 mm long and 1.5–2 mm wide, glabrous, the ovules 6–8-seriate in each locule; disc short, pulvinate. *Capsule* compressed-orbicular, often shallowly emarginate at the tip and truncate to broadly but shallowly subcordate basally, 3.2–5.8 cm long and 3.7–5.5 cm wide, drying reddish brown, the margins not undulate, seeds thin, 0.9–1.2 cm long and 1.1–1.7 cm wide, the wing more or less surrounding and clearly demarcated from the seed body, hyaline-membranaceous with brownish streaks.

This species is commonly cultivated in the Costa Rican uplands and probably also in Chiriquí Province, although I have seen no Panamanian specimens. As interpreted by Sandwith (Kew Bull. 1953: 455. 1954) it has a restricted natural range in northwestern Argentina. However, it is widely cultivated throughout the tropics and subtropics of the world. It is closely related to the earlier-described *J. acutifolia* H.B.K., from which it can be distinguished by its larger fruits, shorter calyx, and greater number of pinnae per leaf.

The naming of this species represents a fantastic coincidence in which the same plant was described in two different publications under two different names on the same day (June 1, 1822). Don was the first to unite *J. ovalifolia* with his *J. mimosifolia* so his choice of names must be accepted.

16. KIGELIA

Kigelia DC., Rev. Bign. (Bibl. Univ. Genève) 19. 1838, nom. cons.

Medium-sized *trees* with spreading crowns. Leaves imparipinnately compound, usually 7–9-foliolate. *Inflorescence* a pendulous racemose panicle with the central axis greatly elongated, hanging flagelliflorously below lower branches. *Flowers* with the calyx large, cupular, irregularly 5-toothed; corolla brownish maroon, campanulate above a tubular base; stamens more or less didynamous, the anther thecae not divergent; ovary cylindrical, lepidote; disc large, annular-pulvinate. *Fruit* very large, indehiscent, cylindrical-oblong, fibrous and woody, to 12 cm or more in diameter, commonly to 50 cm long; seeds flat, wingless, the cotyledons folded in half along their central axis.

Probably only one species of tropical African savannas.

1. **Kigelia pinnata** (Jacq.) DC., Rev. Bign. (Bibl. Univ. Genève) 24. 1838. —FIG. 16.

Crescentia pinnata Jacq., Collect. 3: 203, *tab. 18.* 1791. TYPE: (not seen).
Tanaecium pinnatum (Jacq.) Willd. *in* L. Sp. Pl., ed. 4. 3: 312. 1802.

Tree to at least 15 m tall and 50 cm d.b.h.; crown spreading; twigs pubescent, often hollow. *Leaves* imparipinnately compound, mostly 7–9-foliolate, the leaflets opposite or subopposite, each leaflet elliptic to elliptic-obovate, rounded at the tip and base, 1.9–11.6 cm long and 1.4–6.8 cm wide, proximal leaflets smallest

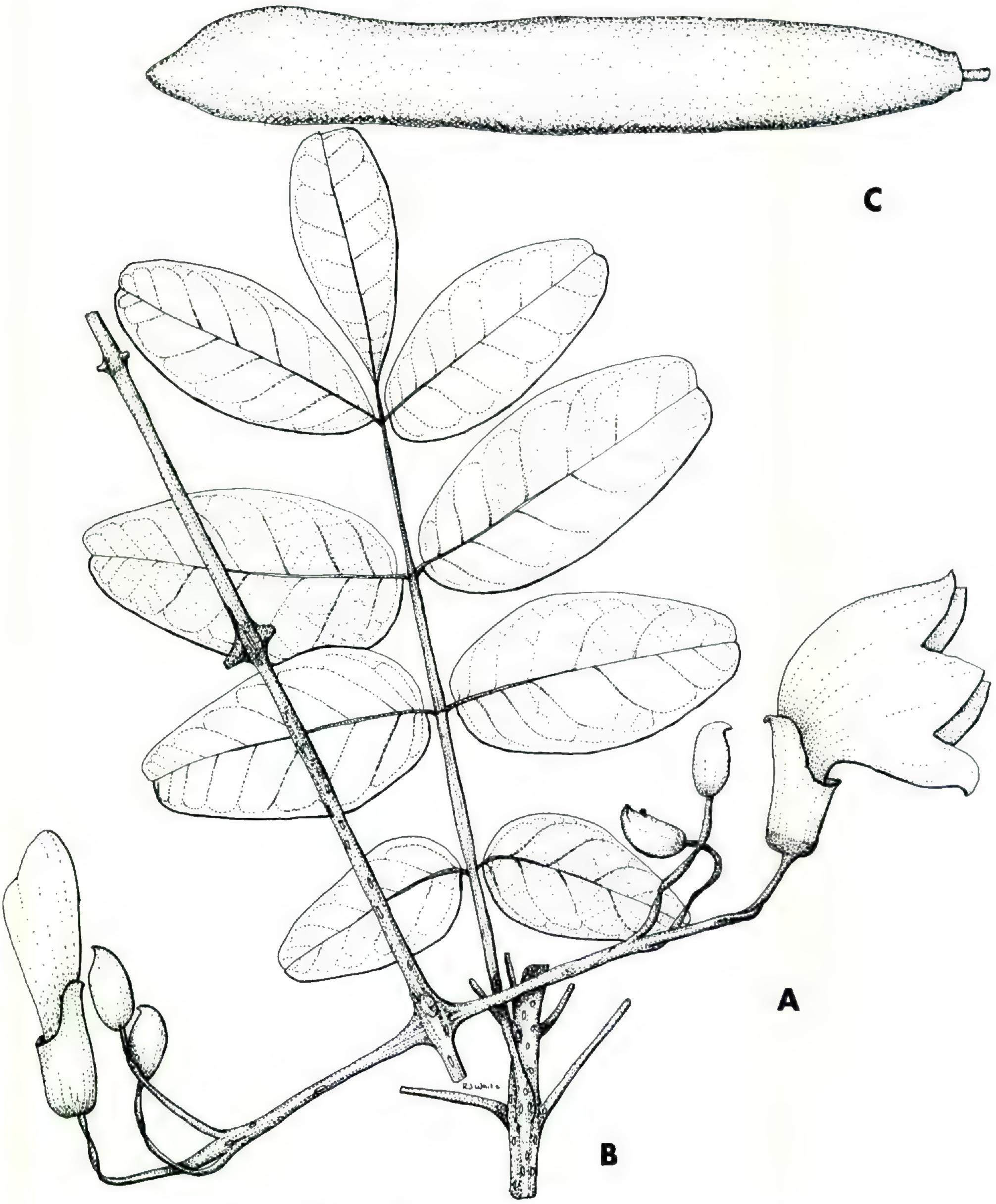


FIGURE 16. *Kigelia pinnata* (Jacq.) DC.—A. Inflorescence (× ½).—B. Leaf (× ½). [After *Tyson & Blum 3454* (MO).]—C. Fruit (× ⅙). [After *Gentry s.n.*, Florida (MO).]

and the terminal leaflet largest, the surface strongly minutely papillose and irregularly lepidote, pubescent with simple trichomes on main veins above and beneath and to some extent over the undersurface, petiole 3.3–4.0 cm long. *Inflorescence* a pendent simple panicle with the central axis greatly elongated, flagelliflorous, hanging below lower branches. *Flowers* with the calyx cupular, irregularly 5-dentate, 2.5–4.5 cm long and 1.6–2.7 cm wide, glabrous or subpuberulous, usually with glandular fields in the upper part; corolla deep maroon

inside, maroon streaked with green outside, campanulate above a tubular base, glabrous with a glandular epidermis, pubescent at the level of stamen insertion, 7–9 cm long and 4–6 cm wide at the top of the tube; stamens didynamous, subexserted, the anther thecae slightly divergent, 7–9 mm long and 1.5 mm wide, the filaments basally pubescent, the longer pair 4.9–5.1 cm long, the shorter pair ca. 4.3–4.5 cm long, the staminode 4–5 mm long, inserted 1.2–1.3 cm above base of tube; pistil 6–6.5 cm long, the ovary cylindrical, 10–11 mm long and 3 mm wide, more or less glandular-lepidote, unilocular with 2 bifid parietal placentae at the top, bilocular with 2 axile placentae in each locule for most of the length, the ovules ca. 10-seriate in each locule; disc very large, annular-pulvinate, 3 mm long and 12–13 mm wide. *Fruit* cylindric with rounded ends, large, pendent, indehiscent, to at least 80 cm long and 8 cm wide, rarely set in Panama.

Native to the wooded savannas of East Africa, this species is widely cultivated as an exotic ornamental throughout the tropical and subtropical regions of the world. The pendulous inflorescence with its large off-maroon flowers makes the "sausage tree" distinctive.

CANAL ZONE: Summit Garden, *Croat 14539* (MO). Balboa near firehouse, *Standley 26895* (MO). Ancón, *Gentry 6053* (MO); *Tyson & Blum 3454* (MO, SCZ).

17. LUNDIA

Lundia DC., Rev. Bign. (Bibl. Univ. Genève) 11. 1838, nom. cons. TYPE: *L. glabra* DC.

Phoenicocissus Mart. *ex* Meisn., Gen. Comm. 209. 1840.
Craterotecoma Mart. *ex* DC., Prodr. 9: 215. 1845. TYPE: *C. parviflora* DC. = *L. erionema* DC.

Lianas; stems with 4 phloem arms in cross section; branchlets terete with interpetiolar glandular fields; pseudostipules inconspicuous or lacking. *Leaves* 3-foliolate, the terminal leaflet often replaced by a simple or trifid tendril. *Inflorescence* an axillary or terminal panicle. *Flowers* with the calyx closed and pointed in bud, splitting calypterately, or sometimes bilabiately, cupular and truncate (or bilabiate) at maturity; corolla white to magenta, tubular-infundibuliform to tubular-campanulate, pubescent outside; anthers densely pubescent, the thecae straight, divaricate, the filaments glabrous or pubescent; pollen grains single, 3-colpate, the exine microreticulate; ovary oblong-conical, densely pubescent, the ovules 2–6-seriate in each locule, the style usually more or less pubescent; disc lacking. *Fruit* an elongate-linear more or less compressed capsule, the valves parallel to the septum, pubescent, the median nerve conspicuously raised, and also to some extent the margins or an area near them; seeds thin, bialate, the wings membranaceous, irregularly hyaline at least at tips.

About 12 species of tropical America ranging from Guatemala and British Honduras to Brazil and Bolivia.

Flowering *Lundia* can be readily recognized by the pubescent anthers. The pubescent fruit is also a good character. When sterile, the slightly ciliate, widely ovate, truncate leaves distinguish *Lundia* from most other Bignoniaceae vines. Its much less pronounced pubescence, blunt (not acuminate) pseudostipules, and

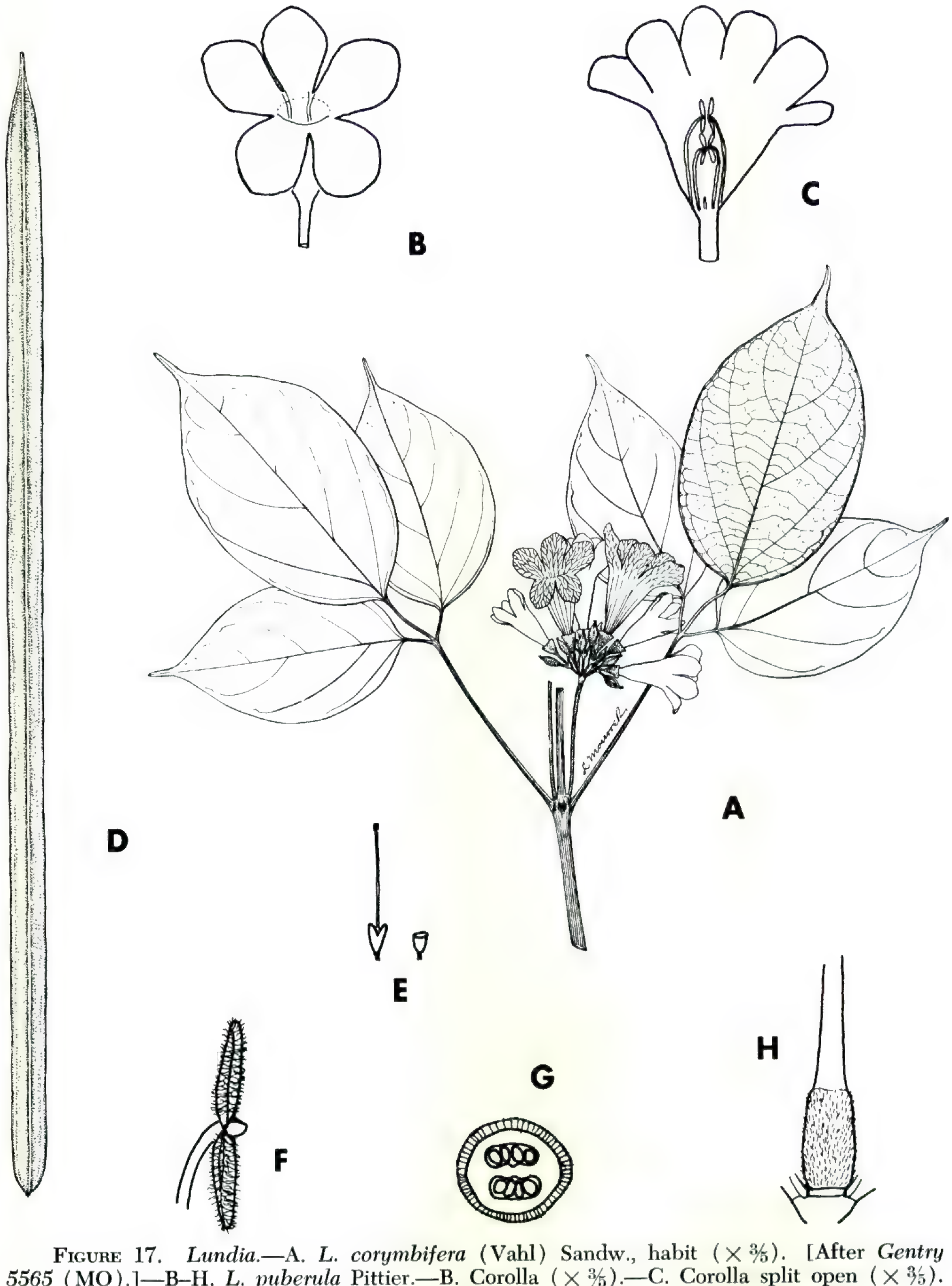


FIGURE 17. *Lundia*.—A. *L. corymbifera* (Vahl) Sandw., habit (× 3/5). [After *Gentry 5565* (MO).]—B–H. *L. puberula* Pittier.—B. Corolla (× 3/5).—C. Corolla split open (× 3/5).—D. Fruit (× 1/5). [After *Gentry 4230* (MO).]—E. Calyces (× 3/5).—F. Anther (× 4 1/5).—G. Ovary cross section (× 15).—H. Ovary (× 6). [After *Gentry & Dressler 1986* (MO).]

mostly wet forest habitat differentiate this genus from the vegetatively similar *Arrabidaea mollissima*.

a. Corolla pink to magenta; style shortly puberulous at the apex or throughout; calyx drying dark, often bilabiate ..... 2. *L. puberula*

aa. Corolla white; style glabrous except at the extreme base; calyx drying tan, almost always evenly truncate ..... 1. *L. corymbifera*

1. **Lundia corymbifera** (Vahl) Sandw., Recueil Trav. Bot. Néerl. 34: 229. 1937.—FIG. 17A.

Bignonia corymbifera Vahl, Eclog. Amer. 2: 45, *pl. 17*. 1798. TYPE: Trinidad, *von Rohr 6* (C).
B. umbrosa H.B.K., Nov. Gen. Sp. Pl. 3: 138. 1819. TYPE: Colombia, Caripa, *Humboldt & Bonpland 279* (P).
Lundia umbrosa (H.B.K.) Bur., Adansonia 8: 282. 1868.
Arrabidaea corymbifera (Vahl) Bur. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 213. 1894.
Cuspidaria corymbifera (Vahl) Baill. *ex* Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894.
Lundia phaseolifolia Rusby, Mem. Torrey Bot. Club 6: 99. 1896. TYPE: Bolivia, Tipuani-Guanae, *Bang 1650* (A, GH, K, MO, NY, US).
L. truncata Rusby, Mem. New York Bot. Gard. 7: 356. 1927. TYPE: Bolivia, Rurrenabaque, *Cardenas 2036* (GH, K, NY, US).
L. valenzuelae Dugand, Mutisia 10: 7. 1952. TYPE: Colombia, Cundinamarca, *Fernandez & Mora 1369* (COL).

Liana to 2.5 cm in diameter; stems with 4 phloem arms in cross section; branchlets terete, drying longitudinally striate, simple puberulous, the nodes with interpetiolar glandular fields; pseudostipules inconspicuous, blunt-conical. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate to elliptic-obovate, acute to acuminate, the base truncate, 6.5–11.5 cm long and 3.3–7.6 cm wide, membranaceous, palmately veined basally, the secondary veins 4–6 on a side, short puberulous at least on main veins above and below and in axils of the lateral nerves beneath, sometimes also with scattered trichomes over the surface, usually more or less lepidote, some plate-shaped glands near the midvein beneath, lepidote glandular basally, drying dark green to brown above, grayish green beneath, never with a macroscopically conspicuous white fringe when young although microscopically ciliate; tendril simple 4–14 cm long; petiolules 1.2–3.2 cm long, petiole 3.2–5.3 cm long, conspicuously simple puberulous. *Inflorescence* a contracted axillary or terminal panicle, the branches strongly simple puberulous. *Flowers* with the calyx in bud terminating in 5 elongate, fused teeth which form an apical point, calypterate with the apical third dehiscent, thus cupular and evenly truncate in mature bud or flower, 3–6 mm long and 4–5 mm wide, puberulous with 1–3-celled simple trichomes; corolla white with the 2 throat ridges yellow, tubular-infundibuliform, 2.5–4.3 cm long and 0.8–1.3 cm wide at the mouth, the tube 1.8–2.8 cm long, the lobes 0.4–1.2 cm long, densely simple puberulous outside, the lobes ciliate margined, glandular-lepidote and puberulous with simple trichomes, the throat mostly glabrous inside, short-puberulous with gland-tipped trichomes at and below the level of stamen insertion; stamens didynamous, the anther thecae divergent to divaricate, 2–3 mm long, the longer filaments 1.3–1.6 cm long, the shorter filaments 0.8–1.2 cm long, the staminode 2–3 mm long, inserted 3–7 mm from base of corolla tube; pistil 1.5–2.4 cm long, the style glabrous except for short appressed trichomes near the base, the ovary tapered cylindric, 2–3 mm long and 1–1.5 mm wide, densely sericeous, the ovules 4-seriate in each locule; disc inconspicuous, 0.5 mm long and 1.5 mm

wide. *Capsule* linear, more or less compressed, velvety pubescent, 29–60 cm long and 1.5–1.9 cm wide, both median nerve and margins distinctly raised; seeds thin, bialate, 1.0–1.3 cm long and 3.4–3.9 cm wide, wings hyaline at the tips, brown at the base, poorly demarcated.

Locally common in tropical wet forest, *L. corymbifera* occurs also in premontane wet forest and parts of the tropical moist forest. It is apparently restricted to the Pacific slope in Central America and ranges from Costa Rica to Bolivia and Brazil. It flowers mostly during the wet season from April or June to October.

Lundia corymbifera is vegetatively different from closely related *L. puberula* in a shorter puberulence, the leaves grayish green below, and branchlets usually drying tannish (not dark). The two species are extremely close and can be distinguished most easily by flower color. The paucity of material of both species makes an understanding of specific delineations difficult.

Lundia valenzuelae Dugand of Colombia is apparently a pubescent variant of this species.

CHIRIQUÍ: Monteverde 2.5 km W of Puerto Armuelles, *Liesner 54* (MO). Río Chiriquí to Remedios, *Woodson et al. 1178* (A, K, MO, NY). Vicinity of Puerto Armuelles, *Woodson & Schery 811* (GH, MO). Vicinity of Bartolome, Peninsula de Burica, *Woodson & Schery 915* (GH, MO, US). DARIÉN: Between Ríos Punusa and Pucro, *Duke 14641* (MO). PANAMÁ: Río Maestro, *Gentry 2236* (MO). 2 mi. E of El Llano, *Gentry 5565* (MO).

2. **Lundia puberula** Pittier, Contr. U. S. Natl. Herb. 18: 258. 15 Sept. 1917. TYPE: Panama, Darién, *Pittier 5499* (F, K, MO, US).—FIG. 17B–H.

L. dicheilocalyx Blake, Contr. Gray Herb. 52: 94. 28 Sept. 1917. TYPE: British Honduras, Toledo, *Peck 495* (GH, K).
L. schumanniana Kränzl., Fedde Repert. 17: 120. 1921. TYPE: Mexico, Campeche, (not seen).
L. colombiana Dugand, Caldasia 4: 236. 1946. TYPE: Colombia, Meta, *Dugand & Jaramillo 3111* (COL, NY).

Liana to at least 2.5 cm in diameter; stems with 4 phloem arms in cross section; the branchlets terete, puberulous, nodes with interpetiolar glandular fields; pseudostipules inconspicuous, blunt. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate, long-acuminate, basally truncate to asymmetrically cordate, 7.4–9.2 cm long and 4.6–5.7 cm wide, membranaceous, palmately veined at the base, the secondary veins 3–5 on a side, sparsely subpuberulous at least on the main veins above and beneath with a few longer trichomes in the axils of lateral nerves beneath and scattered lepidote scales mostly beneath, the margins strongly ciliate, plate-shaped glands near the midvein beneath, lepidote-glandular basally, drying olive brown to reddish-brown; tendril simple, 5–10 cm long; petiolules 2–2.3 cm long, the petiole 2.4–2.9 cm long, puberulous. *Inflorescence* an axillary or terminal panicle, the branches puberulous. *Flowers* with the calyx in young bud conical-pointed, at length truncate, the tip calypterate and evenly dehiscent, or 2(–3)-labiate and the tip splitting, 4–6 mm long and 3–4 mm wide, subpuberulous; corolla pale pink or lavender to magenta, tubular-campanulate or infundibuliform, 3.1–5.8 cm long and 0.7–1.5 cm wide at the mouth, the tube 2.5–4.0 cm long, the lobes 0.8–2.1 cm long, densely simple puberulous outside, the lobes ciliate-margined, glandular-lepidote and puberulous with

simple trichomes inside, the throat glabrous inside or with a few scattered gland-tipped trichomes at and below the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 1.5–2.1 cm long, the shorter pair 1.0–1.3 cm long, the staminode 1–2 mm long, inserted 11–15 mm from the base of corolla tube; pistil 2.9–3.2 cm long, the style somewhat puberulous at least toward the apex, the ovary cylindric, 2.5–3.0 mm long and 1 mm wide, strongly appressed puberulous, the ovules 4-seriate in each locule; disc absent. *Capsule* linear, the valves somewhat compressed, the midvein conspicuously raised, the margins raised but rounded, velvety pubescent, drying blackish, 25–45 cm long and 1.5–1.6 cm wide; the seeds thin, bialate, 0.9–1.2 cm long and 3.3–3.5 cm wide, the wings membranaceous, basally brown, dirty-hyaline at the tip, not clearly demarcated from the seed body.

A seldom-collected species of tropical wet forest and wetter parts of the tropical moist forest, *L. puberula* ranges from British Honduras and southern Mexico to Venezuela. It has been collected in flower in November, January, February, March, and August.

This species is similar to *L. corymbifera*. Although the style of *L. puberula* tends to be pubescent toward the top while that of *L. corymbifera* is pubescent only at the extreme base, this character is variable. The dried calyx of this species is usually dark and bilobed, that of *L. corymbifera* light brown or tan and truncate, but neither of these characters is absolutely constant. Difference in flower color is the best character for separating the two species.

CANAL ZONE: Navy reservation N of Gamboa, *Dressler 3140* (MO). Pipeline Road, *Gentry & Dressler 1986* (MO). COLÓN: Santa Rita Ridge, 1.6 mi. NE of Carretera Transisthmica, *Nee & Mori 3678* (MO); *Gentry & Dwyer 4826* (MO, PMA). DARIÉN: Ridge from top of Cerro Pavarandó to Cerro Venado and Cerro Derumba, *Gentry 4230* (MO). Near La Palma, *Gentry 3933* (MO); *Pittier 5499* (F, K, MO, US).

18. MACFADYENA

Macfadyena A. DC., Prodr. 9: 179. 1845. TYPE: *M. uncinata* (G. Meyer) A. DC. = *M. uncata* (Andr.) Sprague & Sandw.

Doxantha Miers, Proc. Roy. Hort. Soc. 3: 189. 1863. TYPE: *D. unguis-cati* (L.) Miers = *Macfadyena unguis-cati* (L.) A. Gentry.
Microbignonia Kränzl., Notizbl. Bot. Gart. Berlin 6: 380. 1915. TYPE: *M. auristellae* Kränzl.

Lianas; stems irregularly many-armed in cross section, the phloem arms basically 8 but the xylem irregularly fissured as well; roots usually with conspicuously swollen tubers; branchlets terete; interpetiolar glandular fields present or lacking, even in the same species; pseudostipules small, lanceolate to ovate; juvenile plants distinctive, growing closely appressed against a supporting tree, climbing by means of their recurved tendrils; the leaves much smaller and the tendril relatively larger; frequently rooting from the nodes with the adventitious roots helping to affix the slender vine to its support. *Leaves* 2-foliolate, often with a trifid, uncate tendril. *Inflorescence* a contracted axillary few-to several-flowered cyme or panicle, often reduced to a single flower. *Flowers* with the calyx membranaceous, loosely campanulate, truncate to subspathaceous, often

irregularly lobed; corolla yellow, tubular-campanulate, glabrous outside; anthers glabrous, the thecae straight, divaricate; pollen grains 3 colpate, the exine smooth to microreticulate; ovary linear-oblong, minutely lepidote to subpuberulous or glabrate, the ovules 2–4-seriate in each locule; disc more or less annular-pulvinate. *Fruit* a narrow, linear, compressed capsule, the valves parallel to the septum, smooth, the median nerve thin, slightly raised; seeds thin, bialate, the wings not sharply demarcated from seed body, short and brown, or longer and irregularly hyaline at tips.

Two or three species in tropical America ranging from Mexico and the West Indies to northern Argentina and Uruguay. The two Panamanian species can be told from the other Central American genera by their trifid, uncate tendrils which do not become thick and woody with age. *Melloa quadrivalvis* is the only other species with trifid uncate tendrils and its tendrils become conspicuously woody with age. The juvenile plants of both *M. uncata* and *M. unguis-cati* have a growth form quite different from the adults. The juvenile leaves are much smaller and the plants grow strongly appressed to the bark of trees, climbing straight up by means of hooked tendrils.

a. Calyx subspathaceously split, often with an incurved apicule; leaflets long-acuminate; pseudostipules subulate-lanceolate; interpetiolar glandular fields conspicuous; seeds with short wings, shiny and dark blackish brown; swamps mostly below 50 m elevation ..... 1. *M. uncata*

aa. Calyx truncate or subtruncate, without an apicule; leaflets acute or short-acuminate; pseudostipules more or less ovate, usually striate; interpetiolar glandular fields absent or small and inconspicuous; seeds with wings longer and irregularly hyaline at tip; well-drained sites, mostly above 50 m elevation ..... 2. *M. unguis-cati*

1. **Macfadyena uncata** (Andr.) Sprague & Sandw., Recueil Trav. Bot. Néerl. 34: 215. 1937.—Fig. 18F–J.

Bignonia uncata Andr., Bot. Repos. *tab.* 530. 1808. TYPE: (not seen).
B. uncinata G. Meyer, Prim. Fl. Essequeb. 210. 1818. TYPE: Surinam (not seen).
Spathodea uncata (Andr.) Spreng., Syst. Veg. 2: 835. 1825.
S. uncinata (G. Meyer) Spreng., Syst. Veg. 2: 835. 1825.
Bignonia pachyptera DC., Rev. Bign. (Bibl. Univ. Genève) 8. 1838, nomen nudum.
Dolichandra fenzliana Miq., Linnaea 18: 251. 1844. TYPE: Surinam, *Focke 661* (U).
Macfadyena uncinata (G. Meyer) A. DC., Prodr. 9: 180. 1845.
Pachyptera puberula DC., Prodr. 9: 175. 1845. TYPE: Brazil, Cujaba, *Manso 10* (G-DC).
Spathodea hispida DC., Prodr. 9: 205. 1845. TYPE: Brazil, Cujaba, *Manso 105A* (G-DC).
S. mollis Sond., Linnaea 22: 561. 1849. TYPE: Brazil, *Regnell II.192.* (not seen).
Macfadyena fenzliana (Miq.) Miq., Stirp. Surinam. Select. 125. 1850.
M. hispida (DC) Seem., Jour. Bot. 1: 227. 1863.
M. mollis (Sond.) Seem., Jour. Bot. 1: 227. 1863.
M. pubescens S. Moore, Trans. Linn. Soc., Bot., ser. 2. 4: 418. 1895. TYPE: Brazil, Iter Mattogrossensis, *Moore 1021* (BM).
M. guatemalensis Blake, Contr. U. S. Natl. Herb. 24: 24. 1922. TYPE: Guatemala, Izabal, *Blake 7845* (US).

Liana to at least 2.5 cm in diameter, the bark fibrous, stem with phloem irregularly many-armed in cross section; dimorphic, the juvenile plant with small leaflets, ca. 1.5–3 cm long, climbing straight up tree trunks, often rooting at nodes; branchlets terete, glabrous to puberulous, interpetiolar glandular fields usually present on young twigs, rarely on fertile branches; pseudostipules subu-

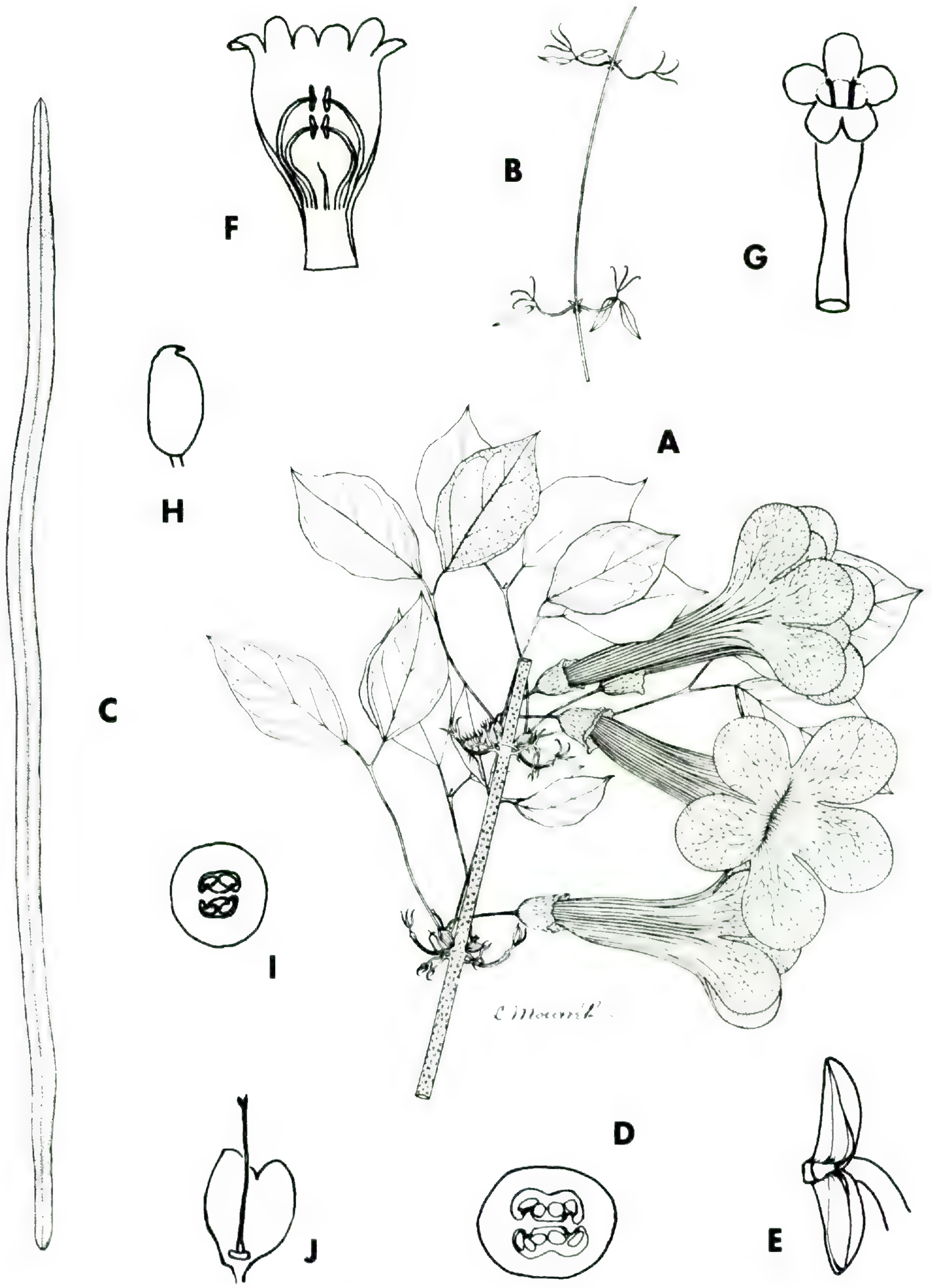


FIGURE 18. *Macfadyena*.—A–E. *M. unguis-cati* (L.) A. Gentry.—A. Habit (× 3/5). [After *Woodson et al. 736* (MO).]—B. Juvenile habit (× 3/5). [After *Gentry 715B* (MO).]—C. Fruit (× 2/5). [After *Croat 14062* (MO).]—D. Ovary cross section (× 15).—E. Anther (× 4 4/5).—F–J. *M. uncata* (Andr.) Sprague & Sandw.—F. Corolla split open (× 3/5).—G. Corolla (× 3/5).—H. Calyx in bud (× 3/5).—I. Ovary cross section (× 12).—J. Pistil and disc (× 3/5). [After *Gentry 1745* (MO).]

late-lanceolate, ca. 2 mm long. *Leaves* 2-foliolate, often with a tendril, especially when young; leaflets when young narrowly ovate to lanceoate, mucronate, basally rounded, when mature narrowly ovate to ovate or elliptic, long acuminate, more or less cuneate to rounded, 5.1–18 cm long and 2.0–9.2 cm wide, membranaceous, secondary veins 5–8 on a side, minutely papillose and lepidote above and beneath, sometimes simple-puberulous beneath especially along main veins, and more sparsely so above; gray green when dry, the main veins reddish or blackish beneath; tendril trifid, uncate, 0.8–2.0 cm long to branching, the 3 arms thickened, 0.5–1.1 cm long; mature petiolules 0.4–2.7 cm long, petiole 0.8–3.6 cm long, petiole and petiolules glabrous to puberulous. *Inflorescence* of flowers borne singly or in reduced few-flowered panicles in leaf axils. *Flowers* inconspicuously scented, calyx membranaceous, glabrous to somewhat lepidote basally, often with scattered glands, usually spathaceously split with apiculate incurved tip, 1.5–3.0 cm long and 0.6–1.4 cm wide, 1–2 cm from base to base of split; corolla yellow with the longitudinal pleats in throat darker, tubular-campanulate, 4.2–8.8 cm long and 0.8–2.0 cm wide at the mouth, the tube 3.8–6 cm long, lobes 0.7–1.7 cm long, glabrous outside, slightly lepidote on lobes inside, sparsely pubescent with simple trichomes along throat ridges and strongly pubescent with long, gland-tipped trichomes and a few simple trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2.5 mm long, the longer filaments 2.1–2.4 cm long, the shorter filaments 1.6–1.9 cm long, the staminode 1.0 cm long, inserted 15–16 mm above base of corolla tube; pistil 3.5–3.7 cm long, the ovary linear, 2.5–3.0 mm long and 1.0 mm wide, minutely lepidote to glabrate, the ovules 2-seriate in each locule; disc annular-pulvinate, 1 mm long and 3–4 mm wide. *Capsule* linear, acute, compressed, 16–26 cm long and 1.5–1.9 cm wide, the wings woody but thin, dark brown or blackish, not demarcated from the seed body.

Found mostly near the coast in swampy habitats of the tropical wet forest and wetter parts of the tropical moist forest, it is especially common in the fresh water sub-mangrove association just inland from the *Rhizophora-Avicennia-Laguncularia* association. It ranges from Mexico to Brazil. This species flowers irregularly throughout the year. The light, short-winged seeds are probably partly wind-dispersed and partly water-dispersed, being light enough to be blown easily and thick enough to withstand continued immersion.

The spathaceously split calyx is the traditional definitive characteristic of the species. Narrow, subulate pseudostipules, conspicuous interpetiolar glandular fields and especially its usually swampy wet forest habitat distinguish this species from *Macfadyena unguis-cati*. *Macfadyena uncata* is less dimorphic than *M. unguis-cati*, and its juvenile leaves are larger.

The supposed distinctions between *Macfadyena uncata* and *M. mollis* (an earlier name is *M. hispida*) do not have specific value. Ecology of these two so-called species seems identical. Although there may be two taxa, I cannot at present justify recognition of more than one in Central America.

BOCAS DEL TORO: Region of Almirante, *Cooper 191* (F, NY). Banks of Río Changuinola, *Dunlap 513* (F, US). Hillside above Almirante, *Gentry 2696, 2757* (both MO). Isla Colón,

von Wedel 57 (MO). Nances Cay Island, *von Wedel 484* (GH, MO). Water Valley, *von Wedel 654* (MO), *1911* (GH, MO, US). Vicinity of Chiriqui Lagoon, *von Wedel 1251* (GH, MO, US). Old Bank Island, *von Wedel 2110* (GH, MO, US). Fish Creek lowlands, *von Wedel 2380* (GH, MO, US). CANAL ZONE: Chagres, *Fendler 207* (GH, K, MO, US), *200* (K). Along Trinidad River, *Pittier 4003* (BM, NY, US). CHIRIQUÍ: Without locality, *Hart CL115* (K). COLÓN: Camino a Portobelo después del Río Guanche, *Correa & Dressler 1765* (MO, PMA). Vicinity of San Miguel de la Borda, *Croat 9899* (MO, SCZ). W of Portobelo, *Gentry 1745* (MO). Puente de Río Salud, Salud, *Taymes & Carrasquilla 142* (MO). DARIÉN: Río Ucurganti, *Bristan 1132* (MO). Río Jaqué to base of Cerro Pavarandó, *Gentry 4198* (MO). Vicinity of El Real, *Gentry 4315* (MO), *Gentry 4574* (MO). PANAMÁ: San José Island, *Johnston 794* (GH). SAN BLAS: Near Mandinga, *Duke 8883* (MO). Near Puerto Obaldía, *Gentry 1558* (MO).

2. **Macfadyena unguis-cati** (L.) A. Gentry, Brittonia 25: 236. 1973.—FIG. 18A–E.

Bignonia unguis-cati L., Sp. Pl., ed. 1. 2: 623. 1753. TYPE: (not seen).
B. unguiculata Vell., Fl. Flum. 234. 1825; 5: *tab.* 33. 1827. TYPE: Brazil (not seen).
B. exoleta Vell., Fl. Flum. 248. 1825; 6: 30. 1827. TYPE: Brazil (not seen).
B. pseudounguis Desf., Cat. Hort. Paris., ed. 3. 397. TYPE: (not seen).
B. gracilis Lodd., Bot. Cab. *tab. 1705.* 1825. TYPE: (not seen).
B. triantha DC., Rev. Bign. (Bibl. Univ. Genève) 21. 1838, nomen nudum.
B. tweediana Lindl., Bot. Reg. 26: *tab. 45.* 1840, non Griseb. TYPE: *Strangways s.n.*, cultivated in England, imported from Buenos Aires (not seen).
Batocydia unguis (L. emend. DC.) Mart. *ex* DC., Prodr. 9: 146. 1845.
B. exoleta (Vell.) Mart. *ex* DC., Prodr. 9: 148. 1845.
Bignonia unguis L. emend. DC., Prodr. 9: 146. 1845.
B. unguis var. *gracilis* (Lodd.) A. DC., Prodr. 9: 146. 1845.
B. acutistipula Schlecht., Linnaea 26: 375. 1853. TYPE: Mexico (not seen).
Doxantha acutistipula (Schlecht.) Miers, Proc. Roy. Hort. Soc. 3: 190. 1863.
D. adunca Miers, Proc. Roy. Hort. Soc. 3: 188. 1864. TYPE: Based on *Bignonia unguis* Vell.
D. exoleta (Vell.) Miers, Proc. Roy. Hort. Soc. 3: 190. 1863.
D. lanuginosa Miers, Proc. Roy. Hort. Soc. 3: 190. 1863, nomen nudum.
D. mexicana Miers, Proc. Roy. Hort. Soc. 3: 190. 1863, nomen nudum. TYPE: Mexico, *Coulter 1004* (not seen).
D. praesignis Miers, Proc. Roy. Hort. Soc. 3: 190. 1863, nomen nudum. TYPE: San Domingo, *Imray s.n.* (not seen).
D. serrulata Miers, Proc. Roy. Hort. Soc. 3: 190. 1863, nomen nudum. TYPE: Guadeloupe, *Duchassaing s.n.* (not seen).
D. tenuicula Miers, Proc. Roy. Hort. Soc. 3: 190. 1863, nomen nudum. TYPE: Hispaniola, *Swartz s.n.* (not seen).
D. unguiculata (Vell.) Miers, Proc. Roy. Hort. Soc. 3: 190. 1863.
D. unguis (L. emend. DC.) Miers, Proc. Roy. Hort. Soc. 3: 190. 1863.
Bignonia inflata Griseb., Symb. Fl. Argent. 256. 1879. TYPE: Argentina (not seen, CORD fide Fabris, Revista Mus. La Plata, Secc. Bot. 9: 391. 1965).
B. lanuginosa Hemsl., Biol. Centr. Amer. Bot. 2: 491. 1882. TYPE: Mexico, Sierra San Pedro Nolasco, Tolaya, etc., *Jurgenson 478* (K, holotype; BM, isotype).
B. unguis-cati L. var. *guatemalensis* K. Schum. & Loes., Bot. Jahrb. Syst. 23: 130. 1896. TYPE: Guatemala, Retaluleu, *Bernoulli & Cario 2057* (K).
B. unguis-cati L. var. *serrata* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 283. 1896. TYPE: (not seen).
B. californica Brandeg., Zoe 6: 170. 1903. TYPE: Mexico, Baja California, *Purpus 249* (MO, US).
Bignonia unguis-cati var. *exoleta* (Vell.) Sprague, Bull. Herb. Boiss., sér. 2. 5: 84. 1905.
Doxantha unguis-cati (L.) Miers emend. Rehder, Mitt. Deutsch. Dendrol. Ges. 1913: 262. 1913.
Bignonia dasyonyx Blake, Contr. Gray Herb. 52: 93. 1917. TYPE: British Honduras, Toledo, *Peck 919* (GH, holotype; K, isotype).
Doxantha dasyonyx (Blake) Blake, Jour. Bot. 61: 192. 1923.
D. unguis-cati var. *dasyonyx* (Blake) Seib., Carnegie Inst. Washington Publ. 522: 423. 1940.
D. unguis-cati var. *exoleta* (Vell.) Fabris, Revista Mus. La Plata, Secc. Bot. 9: 394. 1965.

Liana to 6 cm in diameter, the bark dark, fibrous, irregularly striate; attached to supporting tree by adventitious rootlets; phloem of stem irregularly many-armed in cross section; dimorphic, the juvenile plant with small leaflets, 1–2 cm long and 4–8 mm wide, climbing straight up tree trunks, often rooting at nodes; branchlets terete, puberulus to glabrous, the nodes usually without interpetiolar glandular fields; pseudostipules ovate, longitudinally striate. *Leaves* 2-foliolate, often with a tendril especially when young; leaflets when young narrowly ovate to lanceolate, mucronate at the tip, basally rounded, when mature narrowly ovate to ovate, acute to acuminate, cuneate to truncate, 5.0–16 cm long and 1.2–6.9 cm wide, membranaceous, secondary veins 4–6 on a side, scattered lepidote above and beneath, otherwise glabrous above and beneath or puberulous especially along main veins, a few plate-shaped glands near midvein beneath, drying dark green or dark olive to almost black, the main veins often reddish below; tendril trifid, uncate, 0.1–3.5 cm long to branching, the 3 arms thickened, 0.3–1.7 cm long; mature petiolules 0.5–2.5 cm long, petiole 1.1–4.7 cm long, glabrous or subpuberulous. *Inflorescence* an axillary panicle usually reduced to 1 or 3 flowers, rarely to 15 flowers in Panama, the branches more or less glabrous. *Flowers* with an odor similar to the leaves of many Rutaceae, calyx membranaceous, cupular with a sinuous margin, subtruncate, glabrous to slightly lepidote, often with scattered glands, 5–18 mm long and 8–18 mm wide; corolla yellow with ca. 9 orange lines in the throat, tubular-campanulate, 4.5–10.0 cm long and 1.2–2.4 cm wide at the mouth, the tube 3.3–6.9 cm long, the lobes 1.2–3.1 cm long, glabrous outside, glabrous or slightly simple puberulous along throat ridges inside, pubescent with simple, jointed trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3 mm long, the longer filaments 1.9–2.4 cm long, the shorter filaments 1.2–1.8 cm long, the staminode 0.5–1.5 cm long, occasionally developed into a fifth stamen, inserted 4–8 mm above the base of the tube; pistil 2.8–3.8 cm long, the ovary linear, 6–7 mm long and 1.2 mm wide, minutely lepidote to subpuberulous, the ovules 4-seriate, but appearing 2-seriate in most cross sections; disc annular, 1–1.5 mm long and 3–4 mm wide. *Capsule* elongate-linear, tapering at the ends, flattened, 26–95 cm long and 1.0–1.9 cm wide, the surface inconspicuously lepidote, drying blackish with small whitish lenticels, midrib not raised; seeds 1.0–1.8 cm long and 4.2–5.8 cm wide, the wings membranaceous, blunt-ended, mostly brown, the extreme tips irregularly hyaline, not sharply demarcated from seed body.

A common vine of the tropical dry forest, this species becomes progressively less common in premontane moist forest and tropical moist forest and rare in premontane wet forest and tropical wet forest. The species is widespread, ranging from Mexico (including Baja California) and the West Indies to Argentina. It flowers mostly during late dry season and early wet season from March to June. The single collection from the premontane wet forest of Panama (lower slopes of Cerro Jefe) was in flower in mid wet season (October). The seeds are dispersed in mid dry season.

Seedlings of *Macfadyena unguis-cati* can persist for extended periods and

are one of the commonest seedlings encountered in tropical dry forest. They normally have one or two pairs of relatively large leaves on a short upright stem followed by production of the small-leaved juvenile growth form, which trails across the ground until it reaches a tree upon which it can climb. This juvenile form is also very abundant. The shift to adult growth form occurs only after the vine escapes the shade of the forest floor and is probably a light-triggered reaction.

When sterile this species is differentiated from *M. uncata* by its ovate, longitudinally striate pseudostipules and the habitat difference. Presence or absence of interpetiolar glandular fields is not a reliable character. Seedlings which lack tendrils and are difficult to recognize can often be identified by a faint sweetish odor in the crushed leaves. The thickened tap root of even tiny seedlings with only four leaves is another character of some use in identification.

CANAL ZONE: Barro Colorado Island, *Croat 9141, 10110, 10224* (all MO), *12498* (MO, SCZ), *12588* (MO), *14062* (MO, SCZ), *14081, 14645* (both MO); *Shattuck 264* (F, MO), *944* (MO); *Wetmore & Vestal 75* (F). Pipeline Road, *Gentry 2094* (MO). S of Pedro Miguel, *Gentry 4865* (MO). Boy Scout road near Madden Lake, *Gentry 5059* (MO). Madden Dam, *Gentry 5066* (MO). Ancón Hill, *Gentry 5125* (MO). Fort Sherman, *Gentry & Tyson 4837* (MO). Vicinity of Ancón, *Piper 6023* (US). Corozal, *Sharp s.n.* (SCZ). Las Cascades Plantation, *Standley 29693* (US). DARIÉN: S of Jaqué, *Gentry 4145* (MO). El Real, *Gentry 4532* (MO). Trail up Cerro Pirre, *Gentry 4591, 4606* (both MO). PANAMÁ: Finca Indio on slopes of Cerro Jefe, *Gentry 2148* (MO). Río Pasiga, *Gentry 2286, 2328, 2366* (all MO). Near Río Espavé, *Gentry 3697* (MO). Ca. 16 km from Bayano crossing on trail to Santa Fé, *Gentry 3807* (MO). Near Madden Lake, *Gentry 5051* (MO). E of Pacora, *Woodson et al. 736* (A, MO, NY). W of Campana, *Woodson et al. 1308* (A, MO, NY). Isla Taboga, *Woodson et al. 1450* (A, MO).

19. MARTINELLA

Martinella Baill., Hist. Pl. 10: 30. 1888. TYPE: *M. martinii* (DC.) Baill. *ex* K. Schum. = *M. obovata* (H.B.K.) Bur. & K. Schum.

Lianas; stems with 4 phloem arms in cross section, the pith large; branchlets terete, without interpetiolar glandular fields, with a conspicuously swollen interpetiolar ridge, this less pronounced but still present when dried; pseudostipules absent. *Leaves* 2-foliolate, often with a trifid tendril, the tendril arms somewhat flexuous. *Inflorescence* an axillary raceme. *Flowers* with the calyx tubular-campanulate, bilabiate or sometimes irregularly 3–4-labiate; corolla deep wine-colored, tubular-campanulate above a narrow tubular base, glabrous to inconspicuously lepidote outside; anthers glabrous, the thecae straight, divaricate; pollen grains single, 3-colpate, the exine finely reticulate; ovary linear-cylindric, sparsely lepidote or puberulous, the ovules (2–)4-seriate in each locule. *Fruit* a strongly compressed linear capsule, the valves parallel to the septum, thin, smooth, the median nerve indistinct; seeds thin, bialate, the wings poorly demarcated, membranaceous, mostly pale brown, lighter at the tips.

About two species of continental tropical America ranging from southern Mexico to Brazil and Bolivia.

1. **Martinella obovata** (H.B.K.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 161, *pl. 84*. 1896.—FIG. 19.

Spathodea obovata H.B.K., Nov. Gen. Sp. Pl. 3: 147. 1819. TYPE: Colombia, Turbaco, *Humboldt & Bonpland 1391* (P).
Bignonia longisiliqua Bert. *ex* Spreng., Syst. Veg. 2: 830. 1825, non Vell. TYPE: Colombia; Río Magdalena (not seen).
B. obovata (H.B.K.) Spreng., Syst. Veg. 2: 830. 1825.
B. fockeana Miq., Linnaea 18: 609. 1844. TYPE: Surinam, Paramaribo, *Focke 924* (U).
Tabebuia cordata Benth., Bot. Voy. Sulphur 129. 1844. TYPE: Panama, Darién, *Barclay s.n.* (K).
Bignonia martinii DC., Prodr. 9: 152. 1845. TYPE: French Guiana, *Martin s.n.* (U, US).
Tabebuia latifolia DC., Prodr. 9: 213. 1845, non Rich. TYPE: French Guiana, collector unknown (G-DC, *ex* P, 1821).
Macfadyena fockeana (Miq.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
M. obovata (H.B.K.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
Martinella martinii (DC.) Baill. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894.
Anemopaegma leptosiphon Rusby, Mem. New York Bot. Gard. 7: 354. 1927. TYPE: Bolivia, Ixiamos, *Cardenas 1926* (NY).
Martinella iquitosensis Samp., Ann. Acad. Brasil Sci. 7: 122. 1935. TYPE: Peru, Loreto, *Kuhlmann 1492* (not seen).
Arrabidaea duckei Samp., Bol. Mus. Nac. Rio de Janeiro, Bot. 12: 81. 1936. TYPE: Brazil, *Ducke s.n.* (R No. 28,626) (not seen).
Periarrabidaea duckei (Samp.) Samp., Ann. Acad. Bras. Sci. 12: 91. 1936.

Liana to at least 7 cm in diameter, the bark smooth, green on the younger branches; stem with 4 phloem arms in cross section, the pith large; branchlets terete to subterete, puberulous with short-gland-tipped trichomes to glabrate, green and smooth when fresh, usually dark when dry, the nodes without interpetiolar glands or pseudostipules, usually conspicuously thickened laterally with a raised ridge connecting opposite petioles. *Leaves* 2-foliolate, sometimes with a tendril; the leaflets ovate to elliptic, acuminate to obtuse, truncate to asymmetrically subcordate, 7.2–21 cm long and 3.3–15.5 cm wide, chartaceous, secondary veins 5–8 on a side, the surface microscopically roughened, sometimes indistinctly and sparsely puberulous along veins, plate-shaped glands irregularly scattered along the midvein beneath, glossy green when fresh, drying grayish green to olive with main veins brownish to tan beneath; tendril usually trifid, 4–23 cm long to branching, the 3 arms 0.2–2.4 cm long; petiolules and petiole often twisted slightly, glabrous to subpuberulous, the petiolules 3.0–6.6 cm long, the petiole 2.9–7.5 cm long. *Inflorescence* an axillary raceme of 1–21 flowers, the branches slightly puberulous. *Flowers* without noticeable odor, calyx tubular-campanulate, 2–4-lipped, 1.1–2.1 cm long and 0.7–1.2 cm wide, inconspicuously puberulous with simple, glandular, or rarely thick-stellate trichomes and/or lepidote scales, without glands; corolla deep wine-colored; campanulate above a narrowed 1.7–2.4-cm-long and 0.4–0.6-cm-wide base, 4.1–6.0 cm long and 0.8–2.1 cm wide at the mouth, the tube 3.5–5 cm long, the lobes 0.6–1.5 cm long; more or less glabrous to glandular-lepidote on the tube outside, simple-puberulous at the base and margin of the lobes outside, stalked-lepidote in the floor of the tube within, the lobes papillate-lepidote inside, pubescent at the level of stamen insertion with short, 1–3-celled, gland-tipped trichomes; stamens didynamous, the anther thecae divaricate, 2.5–3 mm long, the longer filaments 1.5–1.7

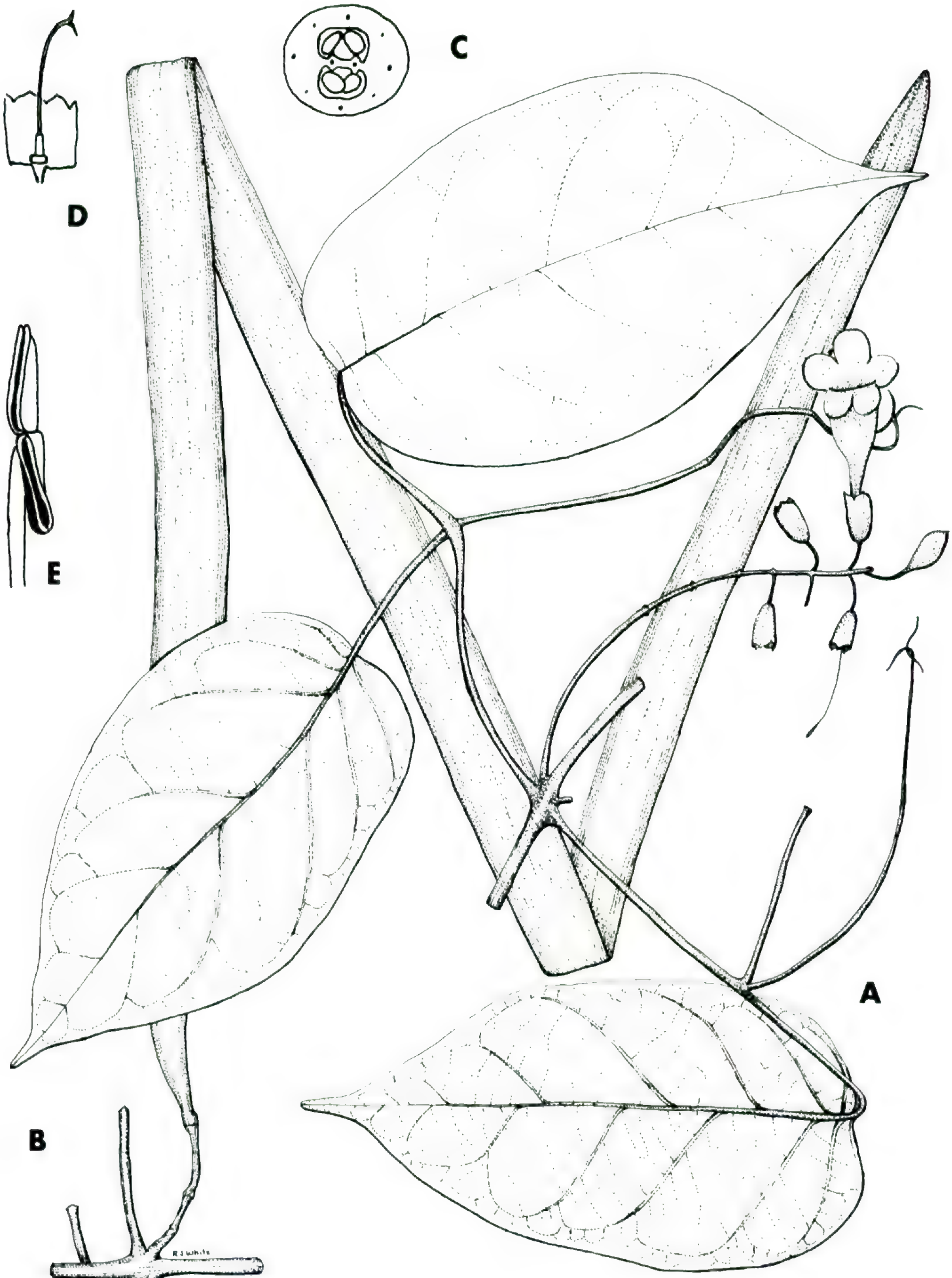


FIGURE 19. *Martinella obovata* (H.B.K.) Bur. & K. Schum.—A. Habit (× ½). [After *Gentry 4981* (MO).]—B. Fruit (× ½). [After *Tyson 5460* (MO).]—C. Ovary cross section (× 10).—D. Pistil and disc (× ½).—E. Anther (× 5). [After miscellaneous fresh material.]

cm long, the shorter filaments 1.1–1.4 cm long, the filaments inserted 14–18 mm from the base of the corolla tube, the staminode 1–2 mm long, inserted 10–11 mm from base of tube; pistil 3.5–3.7 cm long, the ovary linear, 4 mm long and 1.5 mm wide, sparsely lepidote or simple-puberulous, the ovules (2–)4-seriate in each locule; disc annular-pulvinate, 1.5 mm long and 4–5 mm wide. *Capsule* linear, acute, strongly flattened, 55–130 cm long and 1.2–1.8 cm wide, the surface even, finely ridged under a lens, glabrous to inconspicuously subpuberulous, especially near the margins; seeds very thin, 0.9–1.8 cm long and 3.0–5.4 cm wide, the wings symmetrical, blunt-ended, membranaceous but brownish, lighter at the tips, poorly demarcated from the seed body.

A widespread but relatively uncommon vine of tropical wet forest, premontane wet forest, and wetter parts of the tropical moist forest, *M. obovata* ranges from British Honduras to Brazil and Bolivia. It flowers sporadically through the year especially in the wet season.

When sterile this vine is recognized by its glossy, long-petioluled leaves with prominent linear interpetiolar swellings, trifid tendrils, and the tendency of the petioles and petiolules to bend or twist. The flower color is distinctive and the fruits are perhaps the longest (to 190 cm, fide Dugand, Caldasia 7(31): 13. 1955) in the family.

CANAL ZONE: Barro Colorado Island, *Croat 10079, 14064* (both MO), *14105* (MO, NY, SCZ), *14658* (MO). Boy Scout Road near Madden Lake, *Dwyer & Elias 7489* (MO, SCZ). Cerro Gordo near Culebra, *Pittier 3735* (F, US). Chilibre River below Chilibre, *Seibert 1518* (MO, US). CHIRIQUÍ: Near Río Tinta, *Woodson et al. 403* (MO). COLÓN: Santa Rita Ridge, *Gentry 1800* (MO). DARIÉN: Río Piriaque, *Duke 8141* (MO). Río Sabana above Santa Fé, *Duke 14111* (MO). El Real, *Gentry 4534* (MO). Without locality, *Barclay s.n.* (K). PANAMÁ: San José Island, *Erlanson 97, 338* (both GH, NY, US). Río Piragua (Tabardí), *Gentry 2528* (MO). Río Sulugandí, *Gentry 3744* (MO). 0.4 km from Río Bayano crossing on road to Santa Fé, *Gentry 3853* (MO). Río Espavé near junction with Río Bayano, *Gentry 3898* (MO). Between Río Sulugandí and Río Espavé, *Gentry 4981* (MO). Near Madden Lake, *Gentry & Tyson 5037* (MO). San José Island, *Johnston 771* (BM, GH, MO, US). Road to Cerro Azul, *Lazor 5548* (SCZ). Vicinity of Cerro Jefe, *Lewis & Dressler 7566* (MO). Near Río Pacora, *Maurice 815* (US). Macapale Island in Madden Lake, *Tyson 5460* (MO, SCZ). SAN BLAS: Near stream above Puerto Obaldía, *Gentry 1539* (MO).

20. MELLOA

Melloa Bur., Adansonia 8: 379. 1868. TYPE: *M. populifolia* (DC.) Britt. = *M. quadrivalvis* (Jacq.) A. Gentry.

Lianas, stems with phloem irregularly many-armed in cross section; branchlets terete, with or without interpetiolar glandular fields; pseudostipules ovate to almost subulate-acuminate. *Leaves* 2-foliolate, usually with a short, terminal, trifid tendril with recurved claw-like arms, the tendril becoming thickened and woody with age. *Inflorescence* usually a large, open, axillary or terminal panicle, sometimes reduced to a few-flowered cyme, its dichotomies subtended by caducous foliaceous bracts. *Flowers* with the calyx membranaceous, broadly campanulate, obliquely truncate to subspathaceous with a small more or less recurved apicule; corolla yellow, tubular-infundibuliform, glabrous outside; anthers glabrous, the thecae straight, divaricate; pollen grains single,

3-colpate, the exine almost smooth; ovary flattened-ovoid, ribbed, glabrous, the ovules multiseriate in each locule; disc apparently double. *Fruit* a slightly compressed elliptic-oblong capsule, the valves parallel to the septum, woody, very thick (ca. 8 mm), each splitting in the middle at maturity; seeds thin, bialate, the wings hyaline-membranaceous with brown streaks, well demarcated from the seed body.

One species of continental tropical America ranging from Mexico to Argentina.

1. **Melloa quadrivalvis** (Jacq.) A. Gentry, Brittonia 25: 237. 1973.—FIG. 20.

Bignonia quadrivalvis Jacq., Fragm. Bot. 37, *tab. 40*, *fig.* 3. 1800–1809. TYPE: Venezuela, Caracas (not seen).
Spathodea fraxinifolia H.B.K., Nov. Gen. Sp. Pl. 3: 147. 1819. LECTOTYPE: Venezuela, Río Guarico, *Humboldt & Bonpland 780*, flowers only (P).
Bignonia populifolia DC., Prodr. 9: 159. 1845. TYPE: Brazil, Cujaba, *Manso s.n.* (G-DC).
Phryganocydia pisoniana Mart. *ex* DC., Prodr. 9: 209. 1845, pro syn.
Spathodea pisoniana DC., Prodr. 9: 209. 1845. TYPE: Brazil, Bahia, *Martius*, 1818. (M).
Tabebuia pisoniana (DC.) Miers, Proc. Roy. Hort. Soc. 3: 199. 1863.
Tecoma pisoniana DC. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 312. 1897, sphalma for *Spathodea*?
Melloa populifolia (DC.) Britt., Ann. New York Acad. Sci. 7: 188. 1893.

Liana; twigs terete, gray or brown with pale lenticellate flecks, the nodes without interpetiolar glandular fields but often with a ridge connecting opposite petioles; pseudostipules small, deltoid, apiculate. *Leaves* 2-foliolate, sometimes with a tendril or tendril scar; leaflets elliptic, acute to rounded, cuneate to truncate at the base, 5–10 cm long and 2–5.5 cm wide, membranaceous, mostly glabrous, scattered lepidote, inconspicuously scabrous at the extreme base of the midvein above, secondary veins 3–6 on a side, drying olive; tendril trifid, the 3 arms uncate, becoming woody with age; petiolules 0.6–2 cm, the petiole 1.1–3.5 cm long, inconspicuously puberulous, usually drying dark brown. *Inflorescence* an open, few-flowered panicle sometimes reduced to a single dichotomy, each dichotomy subtended by caducous foliaceous bracts 7–21 mm long and 3–6 mm wide, the pedicels 1–3 cm long, drying dark as the inflorescence rachis. *Flowers* with the calyx broadly campanulate, membranaceous, more or less subspathaceous, with an apicule ca. 1 mm long, 10–21 cm long and 9–13 cm wide, glabrous (puberulous in *Spathodea pisoniana*); corolla yellow, tubular, 4–7 cm long and 0.8–1.5 cm wide at the mouth, the tube 3.5–5 cm long, the lobes 0.8–1.5 cm long, mostly glabrous, the lobes more or less ciliate with simple trichomes, conspicuously so in bud, the tube pubescent inside with short trichomes at the level of stamen insertion; stamens didynamous, the thecae divaricate, 4–5 mm long, the longer filaments 2.1–2.3 cm long, shorter filaments 1.4–1.6 cm long, the staminode 5–7 mm long, inserted 5–7 mm from the base of the corolla tube; pistil 3.8–4.0 cm long, the ovary flattened-oblong, conspicuously longitudinally ridged, glabrous, the ovules multiseriate in each locule; disc on a short, thick stalk (hence sometimes described as "double"), 1.5–2 mm long and 3.5–4 mm wide. *Capsule* elliptic, the valves woody, thick (5–8 mm) at maturity breaking evenly in 2 at the midline, drying black or dark brown with tan, lenticellate flecks, minutely tuberculate (sandpaper-finished), 11–15

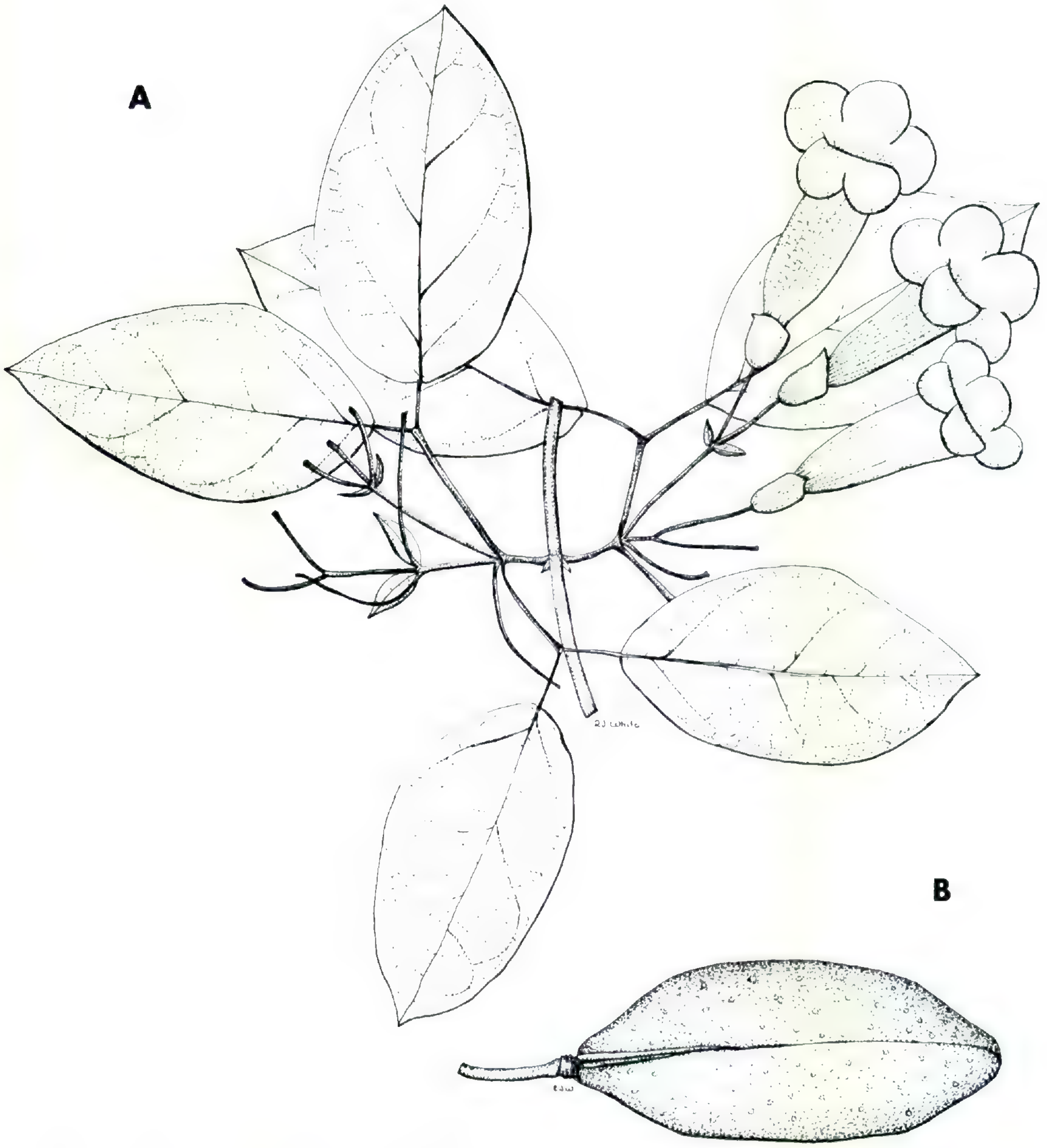


FIGURE 20. *Melloa quadrivalvis* (Jacq.) A. Gentry.—A. Habit (× ½). [After *Hinton et al. 10319*, Mexico (MO).]—B. Fruit (× ½). [After *Irwin et al. 19137*, Brazil (MO).]

cm long and 3.9–5.2 cm wide; seeds thin, bialate, 1.1–1.6 cm long and 3.3–5.5 cm wide, the body brown, the wings hyaline-membranaceous with brown basal streaks well demarcated from the seed body.

Though widespread, ranging from Mexico to Brazil and Argentina, this liana is of only sporadic occurrence through most of its range and is poorly represented in herbaria. It is one of the few species I have not seen in the field, and its ecological parameters remain undertermined. Although not yet collected in Panama, it almost certainly occurs there, having been collected once in Nicaragua, twice in Costa Rica, and once or twice in northern Colombia.

The affinity of *M. quadrivalvis* is with *Macfadyena*, especially with *M.*

unguis-cati, from which it is sometimes difficult to distinguish when in flower. In fact it has been suggested that if *Doxantha* is to be sunk into *Macfadyena*, then perhaps *Melloa* should be also. However, the remarkably different fruit of *Melloa* seems sufficient to maintain its generic separation.

21. MUSSATIA

Mussatia Bur. *ex* Baill., Hist. Pl. 10: 32. 1888. TYPE: *M. prieurei* (DC.) Bur. & K. Schum.

Lianas; branchlets acutely tetragonal with the angles ribbed, interpetiolar glands wanting; pseudostipules large, foliaceous. *Leaves* 2-foliolate, sometimes with a simple tendril. *Inflorescence* a terminal panicle. *Flowers* with the calyx short, shallowly campanulate, truncate, more or less lobed or split; corolla yellow with purplish to brownish stripes, infundibuliform, bilabiate, glandular-lepidote outside; anthers glabrous, the thecae short, divergent to divaricate; pollen grains single, 3-colpate, the exine reticulate; ovary oblong, lepidote, the ovules 4–6-seriate in each locule; disc cupular-pulvinate. *Fruit* an oblong to linear-oblong capsule, the valves parallel to the septum, woody and convex, rugose tuberculate or slightly and inconspicuously short muricate; the seeds thin, bialate, the wings whitish to brownish membranaceous, poorly demarcated.

Two species from southern Mexico to Amazonia.

Useful reference:

Sandwith, N. Y. Notes on tropical American Bignoniaceae. Recueil Trav. Bot. Néerl. 34: 205–232. 1937.

1. **Mussatia hyacinthina** (Standl.) Sandw., Recueil Trav. Bot. Néerl. 34: 218. 1937.—FIG. 21.

Bignonia prieurei DC. sec. Seem., Bot. Voy. Herald 179. 1854, non DC.
Tynnanthus hyacinthinus Standl., Carnegie Inst. Washington Publ. 461: 87. 1935. TYPE: British Honduras, Jacinto Creek, *Schipp S-661* (F, holotype; BM, G, K, isotypes).

Liana to 18 cm in diameter, the bark on smaller stems smooth or somewhat longitudinally striate, light gray to reddish, papery-fibrous in texture, older stems twisted bush ropes with numerous spiral-longitudinal furrows; stem with 8(–16) phloem arms in cross section; branchlets strongly tetragonal with raised ribs on the angles, subscabrous or lepidote, the nodes without glandular fields; pseudostipules foliaceous, more or less ovate, usually acute, 4 at each node, 1.2–2.1 cm long and 0.5–1.7 cm wide. *Leaves* 2-foliolate, sometimes cirrhose; leaflets ovate, acute to acuminate, basally truncate to broadly cuneate, 12.4–23 cm long and 6.2–11.5 cm wide, entire, membranaceous, secondary veins 6–7 on each side, scattered lepidote above and beneath, somewhat puberulous on the depressed midvein above, more or less scabrous on main veins beneath, conspicuously pubescent with long simple trichomes in axils of secondary veins beneath, drying greenish-olive with veins brownish; tendril simple, 12–23 cm long; petiolules 2.4–4.5 cm long, the petiole 5.9–8.1 cm long, lepidote. *Inflorescence* a terminal panicle, its branches lepidote. *Flowers* with the calyx broadly

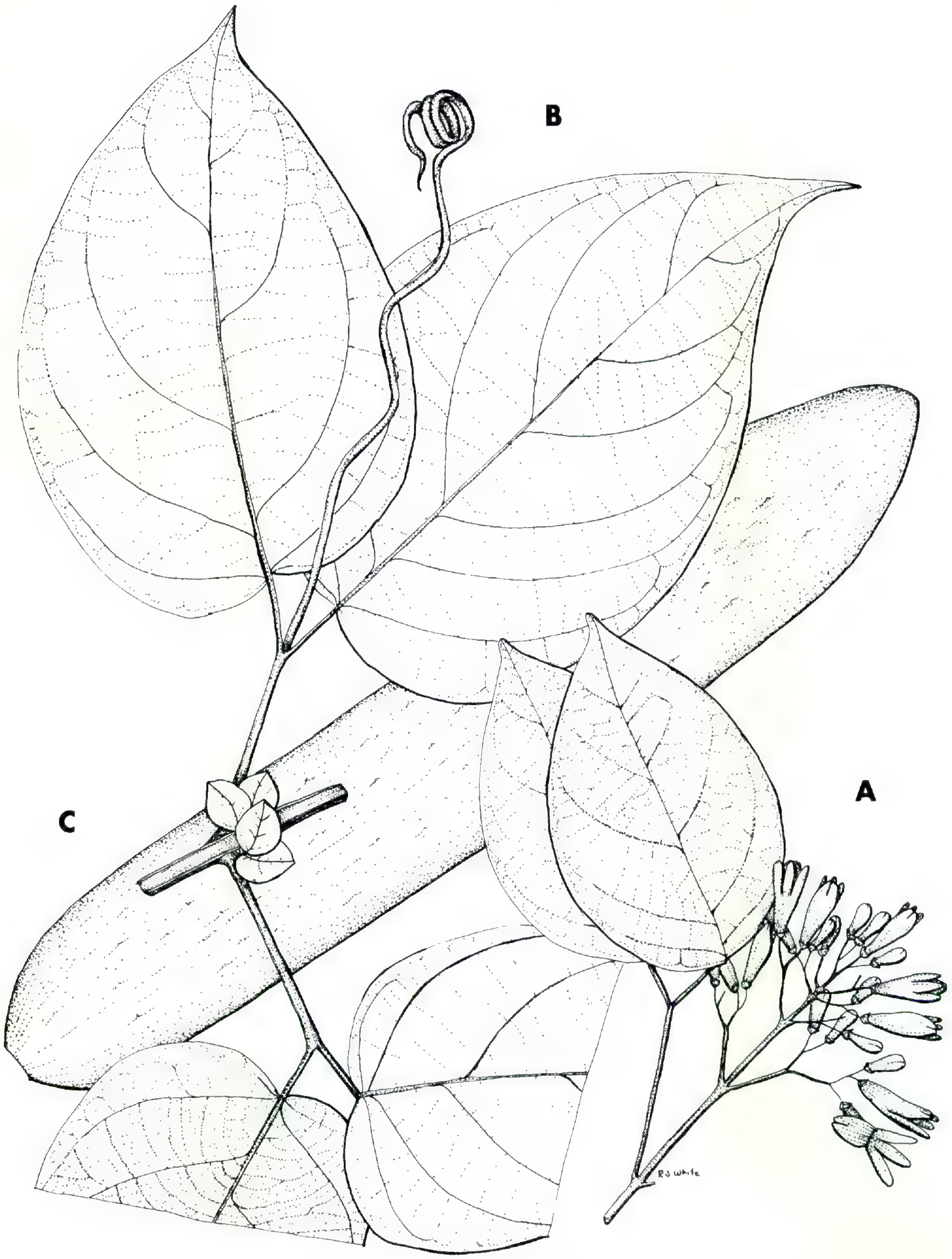


FIGURE 21. *Mussatia hyacinthina* (Standl.) Sandw.—A. Inflorescence (× ½). [After *Tun Ortiz* 992, Guatemala (MO).]—B. Leaves (× ½). [After *Gentry* 2736 and 4527 (both MO).]—C. Fruit (× ½). [After *Gentry* 2736 (MO).]

campanulate, short, 1–2 mm long and 2–4 mm wide, slightly lobed, glabrous, the margin thin; corolla yellow, finely mottled with purple outside, streaked with red or brown inside, infundibuliform, 15–19 mm long and 5–7 mm wide at the mouth, the tube 10–12 mm long, the lobes 5–8 mm long, narrow; the

tube conspicuously glandular-lepidote outside, lobes glandular-lepidote, pubescent at the tips and with a ciliate fringe, the tube lepidote within, lepidote but otherwise glabrous at the level of stamen insertion; stamens didynamous, the anther thecae slightly curved, somewhat divergent to divaricate, 1.0–1.5 mm long, the longer filaments 1.0–1.4 cm long, the shorter filaments 0.8–1.0 cm long, the staminode 5–6 mm long, inserted 1–2 mm from base of corolla tube; pistil 1.4–1.5 cm long, the style bent to follow the posterior curve of corolla, the ovary oblong, densely lepidote, 3 mm long and 1.0–1.5 mm wide, 1.0 mm thick, the ovules 4(–6)-seriate in each locule; disc shallowly pulvinate-cupular, 0.5 mm long and 1.5 mm wide. *Capsule* linear-oblong, obtuse at both ends, the valves woody, flattened but slightly convex, 17.5–29 cm long and 4.4–5.5 cm wide, the surface rough, irregularly warty-tuberculate; seeds 2.2–2.7 cm long and 5.4–6.1 cm wide, the wings wholly light brown, thinly woody at the base to membranaceous at tips, not distinct from the seed body.

A liana of the tropical wet forest and premontane wet forest, it is locally common and reaches gigantic size. It ranges from British Honduras to British Guiana and Peru. The flowers are rarely collected and little known.

The conspicuously square stem with foliaceous pseudostipules is an excellent character for the identification of *Mussatia*. Pubescent leaf axils beneath and relatively thick branchlets distinguish it from *Cydista diversifolia* (H.B.K.) Miers, which has similar stems and pseudostipules. The fruit is similar only to that of *Callichlamys*, which has a smooth capsule valve rather than the slightly tuberculate valve of *Mussatia*.

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2736, 2754* (both MO). COLÓN: W of Portobelo, *Gentry 1770* (MO). DARIÉN: Slopes of Cerro Chucula (drainage of Río Pavarandó), *Gentry 4254* (MO). Between Ríos Cube and Punusa, *Gentry 4470* (MO). El Real, *Gentry 4527* (MO). Near Río Parasenico, *Gentry 4740* (MO). PANAMÁ: Near Río Espavé, *Gentry 3702* (MO). 5–10 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3844* (MO). Near Río Bayano dam site, *Gentry & Tyson 1661* (MO). VERAGUAS: Remedios, *Seemann 1128* (K, P).

22. ONOHUALCOA

Onohualcoa Lundell, Contr. Univ. Michigan Herb. 7: 52. 1942. TYPE: *O. seleri* (Loes.) Lundell = *O. verrucifera* (Schlecht.) A. Gentry.

Bayonia Dugand, Caldasia 4: 62. 1946. TYPE: *B. helicocalyx* (O. Kuntze) Dugand = *Onohualcoa verrucifera* (Schlecht.) A. Gentry.

Lianas, stems with 8 phloem arms in cross section; branchlets terete, glabrate, conspicuously lenticellate, without interpetiolar glandular fields; pseudostipules inconspicuous, when present short and blunt-conical. *Leaves* 3-foliolate, the terminal leaflet often replaced by a trifid tendril. *Inflorescence* a 3–6-flowered corymb in the axil of a young leaf or leaf primordium, these aggregated into many-flowered narrow terminal panicles. *Flowers* with the calyx cupular to tubular-campanulate, 5-ribbed with the ribs ending in elongate (to 5 mm) subulate teeth, puberulous and lepidote; corolla lavender, tubular-campanulate, simple puberulous and glandular-lepidote outside; anthers glabrous, the thecae straight, divaricate; ovary cylindric, more or less glandular-papillate and incon-

spicuously scabrous, the ovules 2-seriate in each locule. *Fruit* a somewhat compressed linear-oblong capsule, the valves parallel to the septum, woody, strongly tuberculate with tubercles to 5 mm long, seeds thick-bodied, bialate, the membranaceous wings basally brown and hyaline at the tips.

One species ranging from southern Mexico to British Guiana and possibly also to Peru and Brazil (fide Sandwith, 1954).

1. **Onohualcoa verrucifera** (Schlecht.) A. Gentry, comb. nov.—Fig. 22.

Bignonia verrucifera Schlecht., Linnaea 26: 655. 1853. TYPE: Venezuela, Curucatí, *Wagener 307* (not seen).
Adenocalymma verruciferum (Schlecht.) Miers, Ann. Mag. Nat. Hist., ser. 3. 7: 393. 1861.
A. helicocalyx O. Kuntze, Rev. Gen. 2: 478. 1891. SYNTYPES: Trinidad, *Kuntze 1153* (K, NY); Venezuela, *Kuntze 1734* (US).
A. moritzii Urb., Fedde Repert. 14: 308. 1916. TYPE: Venezuela, prope Palmar, *Moritz s.n.* (not seen).
Setilobus vicentinus Kränzl., Fedde Repert. 17: 122. 1921. TYPE: St. Vincent, *Caley s.n.* (W).
Adenocalymma fissum Loes., Verh. Bot. Vereins Prov. Brandenberg 65: 102. 1923. TYPE: Mexico, Yucatan, *Seler 4034* (not seen).
A. seleri Loes., Verh. Bot. Vereins Prov. Brandenberg 65: 101. 1923. TYPE: Mexico, Yucatan, *Seler 9901* (not seen).
A. micradenium Standl., Trop. Woods 45: 16. 1936. TYPE: Colombia, La Mojama, *Dugand 611* (F).
Onohualcoa seleri (Loes.) Lundell, Contr. Univ. Michigan Herb. 7: 52. 1942.
Bayonia fissa (Loes.) Dugand, Caldasia 4: 65. 1946.
B. helicocalyx (O. Kuntze) Dugand, Caldasia 4: 63. 1946.
Onohualcoa fissa (Loes.) Sandw., Kew Bull. 1946: 88. 1947.
O. helicocalyx (O. Kuntze) Sandw., Kew Bull. 1946: 87. 1947.
Adenocalymma perezii Standl. & L. O. Wms., Ceiba 3: 61. 1952. TYPE: Honduras, Cortés, *Peréz s.n.* (US).

Liana to at least 8 cm in diameter, the bark smooth, gray with vertical rows of raised brownish lenticels; wood somewhat rank-smelling; stem with 8 phloem arms in cross section; twigs subterete, glabrous to subpuberulous, when dry longitudinally ridged and dark with pale lenticels, the nodes without interpetiolar glandular fields; pseudostipules inconspicuous, blunt-conical. *Leaves* 3-foliolate or 2-foliolate with tendril or tendril scar; leaflets ovate-elliptic, acute, basally more or less cuneate to broadly subcordate, 7.1–13.5 cm long and 3.8–6.3 cm wide, membranaceous, 3-nerved from the base, the secondary veins 4–8 on a side, glabrous to puberulous above and beneath, usually puberulous at least at the base of the midvein with glandular fields at the base and apex of the midvein beneath, also with a few scattered plate-shaped glands, more or less olive when dry (young leaves drying black); tendril trifid, 8–14 cm long to branching, the arms 1–1.4 cm long; terminal petiolule 2.5–4.2 cm long, the lateral petiolules 1.5–2.2 cm long, the petiole 3.7–8.7 cm long, puberulous. *Inflorescence* a 2–6-flowered corymb in the axil of a young leaf or leaf primordium, these aggregated into many-flowered narrow terminal panicles, the branches puberulous. *Flowers* with sweet aroma, calyx cupular, the 5 main ribs ending in narrow, elongate (to 5 mm) teeth, puberulous and lepidote, glandular, 5–7 mm long (without teeth) and 5–6 mm wide, the surface minutely roughened, subverrucose; corolla pinkish lavender with a white throat; tubular-campanulate above an 8 mm by 3 mm tubular base, 5.4–8.1 cm long and 1.0–1.9 cm wide at

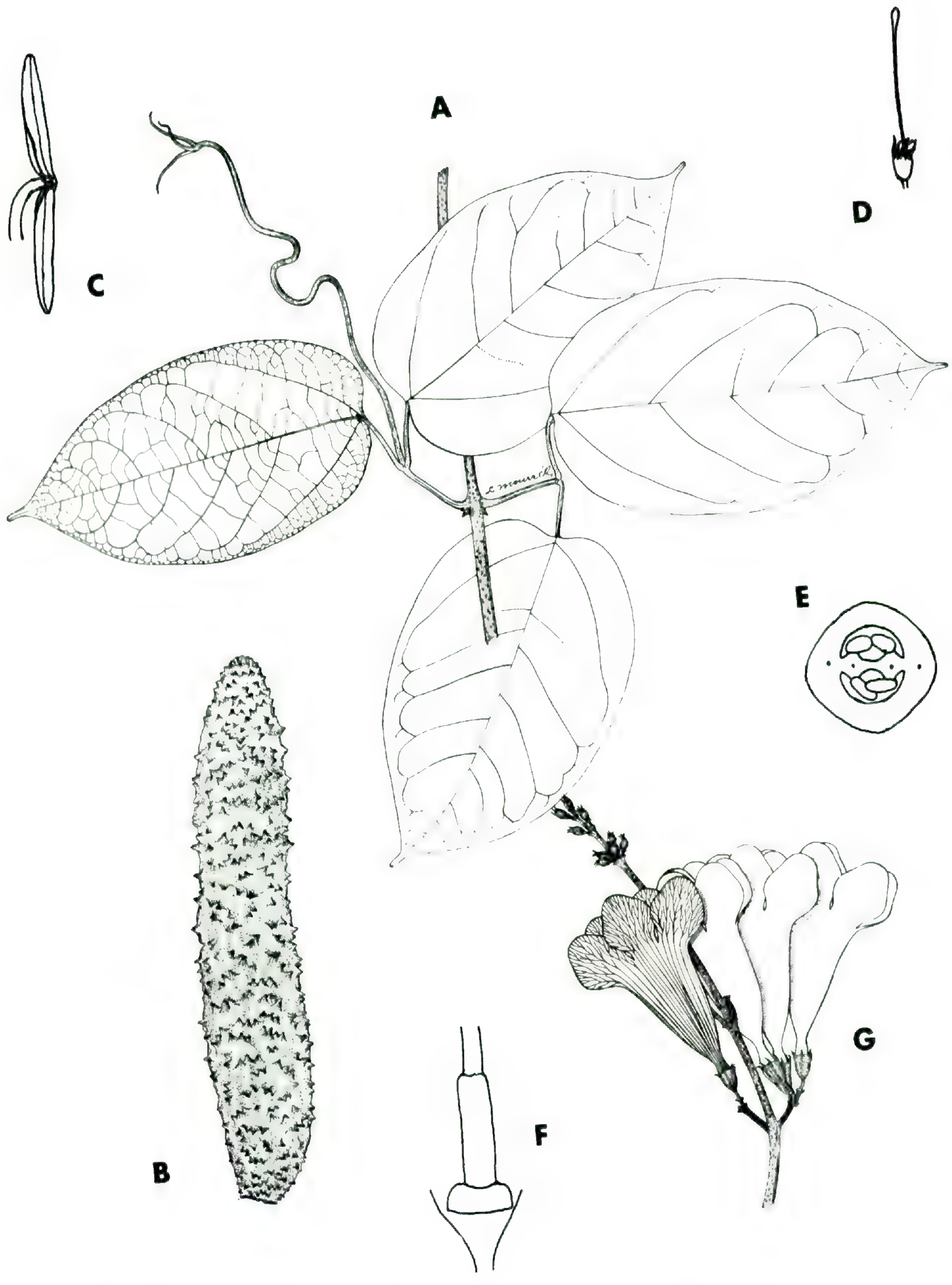


FIGURE 22. *Onohualcoa verrucifera* (Schlecht.) A. Gentry.—A. Habit (× ½).—B. Fruit (× 3/10). [After *Pittier 11100*, Venezuela (VEN).]—C. Anther (× 4).—D. Calyx and pistil (× ½).—E. Ovary cross section (× 12½).—F. Ovary and disc (× 3). [After *Gentry & Tyson 5025* (MO).]—G. Inflorescence (× ½). [After *Pittier 14288*, Venezuela (VEN).]

the mouth, the tube 3.5–6.0 cm long, the lobes 1.2–2.5 cm long; simple puberulous and glandular-lepidote outside, less so on the lobes, mostly glabrous within but somewhat glandular-lepidote on lobes and pubescent at the level of stamen insertion with long, simple, in part gland-tipped, multicellular trichomes; stamens didynamous, the anther thecae divaricate, 3.5–5 mm long, the longer filaments 2.3–2.4 cm long, the shorter filaments 1.1–1.6 cm long, the staminode 4–5 mm long, inserted 8–10 mm from the base of the corolla tube; pistil 3.5–4.2 cm long, the ovary cylindric, 5 mm long and 1–1.5 mm wide, more or less glandular-papillate and inconspicuously scabrous, the ovules 2-seriate in each locule; disc pulvinate, 1 mm long and 3–4 mm wide. *Capsule* linear-oblong, 17–30 cm long and 2.3–2.6(–3.8) cm wide, the surface strongly tuberculate; seeds 1.5–2.5 cm long and 4–7.8 cm wide, bialate, the wings hyaline-membranaceous at the ends, basally brown and coriaceous, merging with the thick woody seed body.

An uncommon but widespread plant of the tropical wet forest and wetter parts of the tropical moist forest, this species ranges from southern Mexico to Venezuela and British Guiana.

The Mexican population has heretofore been regarded as geographically separated and specifically distinct from the plants of northern South America. However, recent collections of this species from Honduras, Costa Rica, and Panama remove the range disjunction and are more or less intermediate morphologically as well. The variation in tubercle length is clinal, and the plants are best treated as a single species.

I have followed a suggestion of Sandwith (1954) in adopting the basionym *Bignonia verrucifera* Schlecht., which is older than *O. helicocalyx* (O. Kuntze) Sandw., which has been in general use for this plant. I have not been able to locate type material of *Bignonia verrucifera*, but the description agrees with this species and does not fit any of the other species known from the type locality in northern Colombia.

CANAL ZONE: Pipeline Road, TTC transect 1, *Gentry 7391* (MO). COLÓN: Above Portobelo Road, *Gentry 1763* (MO). PANAMÁ: Near Madden Lake, *Gentry 5050* (MO); *Gentry & Tyson 5025* (MO). SAN BLAS: Mainland opposite Playón Chico, *Gentry 6372* (MO).

23. PACHYPTERA

Pachyptera DC. *ex* Meisn., Gen. 1: 299; 2: 207. 1840. LECTOTYPE: *P. foveolata* DC. = *P. kerere* (Aubl.) Sandw.

Pseudocalymma Samp. & Kuhlm., O Campo (Rio de Janeiro) 4(11): 15. 1933; Bol. Mus. Nac. Rio de Janeiro 10: 101. 1934. TYPE: *P. laevigatum* (Bur. & K. Schum.) Samp. & Kuhlm. = *Pachyptera hymenaea* (DC.) A. Gentry.

Lianas; stems with 4 or 8 phloem arms in cross section; branchlets terete to subtetragonal, outer cortex thin and tending to peel; often with conspicuous interpetiolar glandular fields; pseudostipules subulate, usually vertically 2–3-seriate. *Leaves* 2–3-foliolate, the petiole usually with an apical glandular field, the terminal leaflet often replaced by a trifid tendril or a simple tendril with a peltate disc at its tip. *Inflorescence* an axillary or terminal panicle or raceme.

Flowers with the calyx cupular to campanulate, truncate, often with plate-shaped glands in the upper part; corolla white to purple, tubular to campanulate, puberulous outside at least on the lobes; anthers glabrous or villous, the thecae divaricate, curved or straight; pollen grains 3-colpate, the exine finely reticulate; ovary cylindric, pustular-lepidote to papillate, the ovules 2(?–4)-seriate. *Fruit* a pale brown capsule, the valves parallel to the septum, extremely flat and compressed to thick and convex with a conspicuously raised midline; the seeds thin with pale translucent papery wings or thick, corky, and essentially without wings.

About seven species in continental tropical America ranging from Mexico to Brazil.

a. Tendrils simple, disc-tipped; leaflets less than 3 cm long ..... 3. *P. parvifolia*
aa. Tendrils trifid, not disc-tipped; leaflets more than 4 cm long.
  b. Vegetative parts without onion odor; pseudostipules acute, vertically 3-seriate; leaves mostly 3-foliolate; inflorescence a short-pedicelled raceme; corolla puberulous outside on tube and lobes; anther thecae villous.
    c. Capsule valves thick, woody, convex, the median nerve conspicuously raised; seeds thick, corky, essentially wingless ..... 2a. *P. kerere var. kerere*
    cc. Capsule valves thin and perfectly flat or slightly raised along the margin, median nerve not obvious; the seeds thin, bialate, with broad papery wings (not yet seen from Panama) ..... 2b. *P. kerere var. incarnata*
  bb. Vegetative parts with conspicuous onion or garlic odor; pseudostipules short, blunt, relatively inconspicuous; leaves 2-foliolate; inflorescence a panicle or few-flowered open raceme; corolla puberulous outside only on lobes; anther thecae glabrous.
    d. Calyx large, more than 13 mm long and 13 mm wide, red violet when fresh; inflorescence an elongate, open, few-flowered panicle or raceme; one pair of anthers exserted; fruits strongly compressed, the median nerve obscure; leaflets elliptic, with glandular fields in the axils of basal lateral nerves beneath ..... 4. *P. standleyi*
    dd. Calyx small, less than 7 mm long and 7 mm wide, greenish when fresh; inflorescence usually a more or less contracted panicle; anthers included; fruits only somewhat compressed, the median nerve conspicuous, raised; leaflets ovate to elliptic, with or without concentration of glands in axils of basal lateral nerves beneath ..... 1. *P. hymenaea*

1. **Pachyptera hymenaea** (DC.) A. Gentry, Brittonia 25: 236. 1973.

Bignonia hymenaea DC., Prodr. 9: 158. 1845. TYPE: Brazil, Bahia, *Blanchet 1434* (G-DC, P).

Anemopaegma pachypus K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 215. 1894, sphalma *platypus*. TYPE: Peru, San Martín, *Spruce 4475* (K).

Bignonia laevigata Kl. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 113. 1896, pro syn.

Adenocalymma laevigatum Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 113. 1896, non Mart. *ex* DC. SYNTYPES: Brazil, Rio de Janeiro, *Sellow L.317* (not seen); Brazil, *Langsdorf s.n.* (not seen), *Glaziou 9529* (F, K, MO).

A. pachypus (K. Schum.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 110. 1896.

A. pohlianum Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 114. 1896. TYPE: Southeast Brazil, *Pohl 1817* (K).

A. macrocarpum Donn. Sm., Bot. Gaz. (Crawfordsville) 40: 9. 1915. LECTOTYPE: El Salvador, San Vicente, *Shannon 5055* (US).

A. obovatum Urb., Fedde Repert. 14: 307. 1916. TYPE: Haiti, Mackenzie, *Duss 1913* (not seen).

A. ciliolatum Blake, Contr. Gray Herb. 52: 90. 1917. TYPE: Nicaragua, León, *Baker 2424* (GH, holotype; MO, NY, US, isotypes).

A. hosmeca Pittier, Contr. U. S. Nat. Herb. 18: 256. 1917. TYPE: Costa Rica, Guanacaste, *O. Jimenez 374* (US).

Petastoma langlasseanum Kränzl., Fedde Repert. 17: 56. 1921. TYPE: Mexico, Nusco, *Langlasse 738* (K, P, US).
P. tonduzianum Kränzl., Fedde Repert. 17: 56. 1921. TYPE: Costa Rica, Guanacaste, *Tonduz 13830* (BM, CR, K, P, US).
Adenocalymma alboviolaceum Loes., Verh. Bot. Vereins Prov. Brandenburg 65: 100. 1923. TYPE: Mexico, Oaxaca, *Seler 1664* (GH, US).
Pseudocalymma laevigatum (Bur. & K. Schum.) Samp. & Kuhl., Bol. Mus. Nac. Rio de Janeiro 10: 101, f. 1934.
P. hymenaeum (DC.) Sandw., Candollea 7: 247. 1937.
P. langlasseanum (Kränzl.) Sandw., Recueil Trav. Bot. Néerl. 34: 210. 1937.
P. macrocarpum (Donn. Sm.) Sandw., Recueil Trav. Bot. Néerl. 34: 210. 1937.
P. pachypus (K. Schum.) Sandw., Recueil Trav. Bot. Néerl. 34: 210. 1937.
P. pohlianum (Bur. & K. Schum.) Sandw., Recueil Trav. Bot. Néerl. 34: 211. 1937.
P. alliaceum var. *microcalyx* Sandw., Kew. Bull. 1953: 467. 1954, pro parte, typo excluso.

Liana to at least 5 cm in diameter, bark smooth, gray; stem with 4–8 phloem arms in cross section; all parts with strong garlic odor; branchlets subterete, glabrous or sparsely lepidote, the nodes with interpetiolar glandular fields; pseudostipules small, flattened-conical. *Leaves* 2-foliolate, usually with a tendril or tendril scar; leaflets ovate to widely ovate, obtuse to acute, basally (Panama) more or less truncate to shallowly cordate, 4.8–9.4 cm long and 3.3–7.5 cm wide, membranaceous, more or less 3-veined from the base, the secondary veins 3–6 on a side, mostly glabrous above and beneath, slightly lepidote at least at the base, often with a glandular field in the axil of the basal nerve pair beneath, drying olive; tendril shortly trifid, 10–14 cm to branching, the 3 arms 0.1–0.4 cm long; petiolules 1.0–2.6 cm long, petiole 1.3–3.5 cm long, petiole and petiolules lepidote, sometimes puberulous at their junction, the petiole sometimes with an apical glandular field. *Inflorescence* a usually more or less contracted panicle terminal on a young shoot, the branches puberulous. *Flowers* with the calyx cupular, truncate or minutely 5-denticulate with the extreme edge membranaceous, 4–6 mm long and 4–6 mm wide, slightly lepidote to puberulous, drying with glandular light spots; corolla lavender to magenta or almost white, tubular-campanulate, 4.1–5 cm long and 0.8–1.5 cm wide at the mouth, the tube 3.0–3.6 cm long, the lobes 0.6–1.3 cm long, the lobes puberulous, tube mostly glabrous inside and out, inconspicuously pubescent at the level of stamen insertion; stamens didynamous, included, the anther thecae somewhat divergent, 3 mm long, the longer filaments 1.8–1.9 cm long, shorter filaments 1.2–1.4 cm long, the staminode ca. 2 mm long, inserted 5–7 mm from base of corolla tube; pistil 2.4–2.6 cm long, the ovary linear-tetragonal, 5–7 mm long and 1 mm wide, lepidote, the ovules 2-seriate in each locule; disc annular-pulvinate, 1 mm long and 2 mm wide. *Capsule* linear, long-acuminate, flattened, 15–25 cm long and 1.7–2.0 cm wide, the surface smooth, glabrous to inconspicuously lepidote with a conspicuously raised central rib, drying tan with scattered small blackish dots; seeds thin, bialate, 1.1–1.5 cm long and 3.1–3.5 cm wide, the wings membranaceous, pale brown at the base, whitish to subhyaline at the tip.

A common liana of the tropical dry forest occurring also sporadically in the tropical moist forest, it ranges from Mexico to Brazil. This species flowers in the dry season from February through March. The seeds are dispersed at the end of the dry season.

The characteristic pungent odor has led to its inclusion in the native pharmacopeia. The Cuna Indians of Panama (*Duke 10854*) put it on their heads to prevent bad dreams. It is one of the few Bignoniaceae vines to receive a common name other than the general term "bejuco" and is known variously as "olmeca," "hosmeca," "jumeca," "ago," or "pedo de padre."

In the field this plant is unmistakable because of its strong onion or garlic odor, and even in the herbarium some of this odor is often maintained. The leaves are also recognizable by their dark green color with pale main veins and their usual wide-ovate shape with a truncate or subcordate base. The fruits can be identified by the combination of long, tapering apex, tan color, and strongly raised midline.

PANAMÁ: Río Agua Clara at Icantí, *Gentry 2596* (MO). San José Island, *Johnston 1342* (GH, MO, US). SAN BLAS: Río Ailigandi, *Duke 10854* (MO). VERAGUAS: Slopes of Cerro Tute W of Santa Fé, *Allen 4442* (GH, MO, NY). WITHOUT LOCALITY: *Hayes 610* (K).

2. **Pachyptera kerere** (Aubl.) Sandw., Recueil Trav. Bot. Néerl. 34: 219. 1937. —FIG. 23A–E.

Bignonia kerere Aubl., Hist. Pl. Guiane Fr. 2: 644, *tab. 260.* 1775, non Lindl. TYPE: French Guiana, *Aublet s.n.* (BM, P-AD no. 12271, W).

B. incarnata Aubl., Hist. Pl. Guiane Fr. 2: 645, *tab. 261, 262, fig. 1–8.* 1775. TYPE: (not seen).

B. heterophylla Willd., Sp. Pl. 3: 298. 1801. TYPE: Based on *B. kerere* Aubl.

Adenocalymma brachybotrys DC., Prodr. 9: 202. 1845. TYPE: French Guiana, *Perrotet s.n.* (P).

Pachyptera foveolata DC., Prodr. 9: 175. 1845. TYPE: French Guiana, *Poiteau s.n.* (G-DC, fragment).

Adenocalymma stridula Miers, Ann. Mag. Nat. Hist., ser. 3. 7: 392. 1864. TYPE: Based on *Bignonia kerere* Aubl.

A. foveolatum (DC.) Baill., Hist. Pl. 10: 7, *fig. 9–16.* 1888.

A. kerere (Aubl.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 119. 1896, pro parte.

Bignonia benensis Britton *ex* Rusby, Bull. Torrey Bot. Club 27: 70. 1900. TYPE: Bolivia, junction of Beni and Madre de Dios Rivers, *Rusby 1143* (NY, US).

Adenocalymma symmetricum Rusby, Descr. 300 Sp. S. Amer. Pl. 122. 1920. TYPE: Venezuela, Lower Orinoco, *Rusby & Squires s.n.* (NY).

Tanaecium zetekii Standl., Contr. Arnold Arbor. 5: 140, *tab. 19.* 1933. TYPE: Panama, Barro Colorado Island, *Woodworth & Vestal 363* (F, holotype; A, MO, US, isotypes).

Pachyptera kerere var. *erythraea* Dugand, Caldasia 7(31): 16. 1955. TYPE: Colombia, Santander, *Romero-Castañeda 4727* (COL).

Liana to at least 5 cm in diameter, the bark gray, smooth; stem with 4 phloem arms in cross section; twigs subtetragonal, longitudinally striate, glabrous to subpuberulous, interpetiolar glands conspicuous; pseudostipules vertically 3-seriate, acute. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate, long-acuminate to acute, broadly cuneate to narrowly subcordate, membranaceous, secondary nerves 6–10 on a side, scattered lepidote below, less so above, puberulous along main veins above and beneath, sunken plate-shaped glands usually conspicuous on both surfaces, olive to brownish when dry, usually darker above; tendril trifid, 8–16 cm long to branching, the three arms 0.2–4.0 cm long, often unequal; terminal leaflet 9–24 cm long and 3.4–10 cm wide, the laterals 7.8–22 cm long and 2.4–9.2 cm wide; terminal petiolule 1.5–6.1 cm long, the laterals 0.5–3.2 cm long, the petiole 0.9–7.1 cm

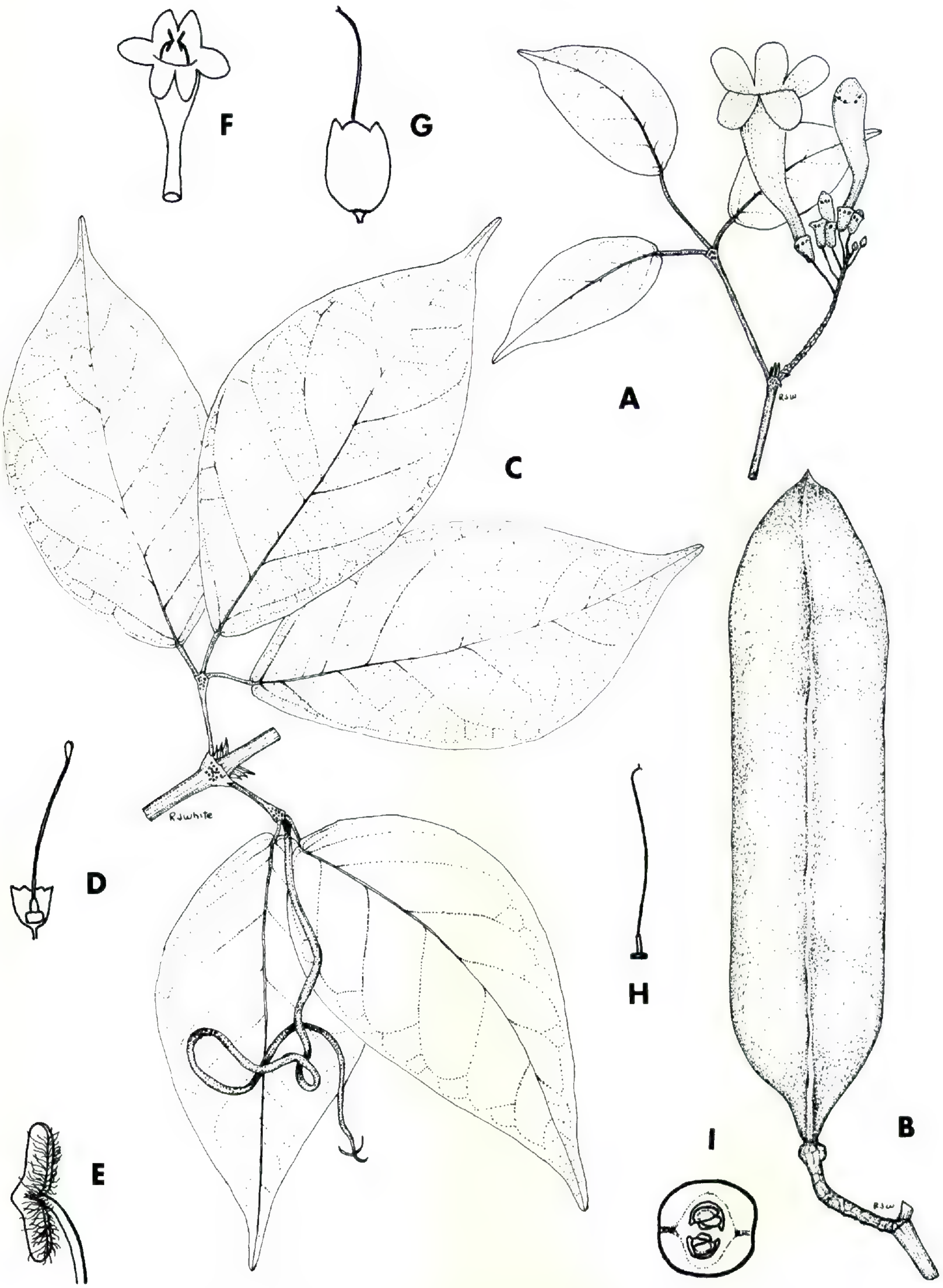


FIGURE 23. *Pachyptera*.—A–E. *P. kerere* (Aubl. emend Splitg.) Sandw.—A. Inflorescence (× ½).—B. Fruit (× ½). [After *Gentry 4401* (MO).]—C. Leaves (× ½). [After *Gentry 4335* (MO).]—D. Pistil and disc (× ½).—E. Anther (× 5).—F–I. *P. standleyi* Steyerm.—F. Corolla (× ½).—G. Calyx (× ½).—H. Pistil and disc (× ½).—I. Ovary cross section (× 12½). [After *Gentry & Tyson 5027* (MO).]

long, above with a conspicuous apical glandular field, scabrous as the petiolules. *Inflorescence* a short axillary or terminal raceme of ca. 10 flowers opening one at a time, the rachis and pedicels puberulous. *Flowers* with the calyx campanulate, irregularly truncate, puberulous, with scattered glands, 7–12 mm long and 5–9 mm wide; corolla white (Panama), tubular-campanulate, 3.6–7.3 cm long and 0.7–1.4 cm wide at the mouth of tube, the tube 3.0–6.3 cm long with a narrowed base 2.3–2.6 cm long and 0.2–0.6 cm wide, lobes 0.5–1.8 cm long, simple puberulous outside with plate-shaped glands at the base of the lobes, inside glandular-lepidote on the lobes and glandular-pubescent below the level of stamen insertion; stamens didynamous, the anther thecae pubescent, each 2–4 mm long, usually bent, the longer filaments 1.9–2.1 cm long, shorter filaments 1.4–1.6 cm long, the staminode 0.3–9.8 cm long, inserted 2.3–2.5 cm above the base of corolla tube; pistil 4.5–4.8 cm long, ovary flattened-cylindric, 2–3 mm long and 1.5–2 mm wide, 1–1.5 mm thick, minutely papillose; disc pulvinate, 1–2 mm long and 3–4 mm wide. *Capsule* (Panama) fusiform-oblong, acuminate at both ends, only slightly compressed, 10.2–22 cm long and 2.4–4.0 cm wide, 1.0–2.4 cm thick, the surface smooth, somewhat glandular and slightly lepidote, the midrib raised; seeds 1.8–2.4 cm long and 2.8–3.8 cm wide, relatively thick and corky, without wings.

A vine restricted almost entirely to lake shores, stream margins, and coastal swamps, *P. kerere* is often common, though seldom collected, in this specialized habitat in the tropical wet forest and wetter parts of the tropical moist forest. It ranges from British Honduras to Amazonian Brazil. This species flowers sporadically throughout the year. The corky, wingless seeds of typical *P. kerere* are water-dispersed.

Striking diagnostic characters include the 3-seriate pseudostipules and the glandular field on the upper surface of the petiole apex. The pubescent anthers are a good floral character.

Two color forms of this species are known in South America, but only the white-flowered form has been recorded in Central America. The red-flowered form has been designated as *P. kerere* var. *erythraea* Dugand. A wind-dispersed form, *P. kerere* var. *incarnata* (Aubl.) A. Gentry, has been collected in Honduras and the Choco of Colombia and will probably be found in Panama. It differs from the typical variety only in its longer, much more compressed fruit and thin, winged seeds.

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2687* (MO). Vicinity of Chiriquí Lagoon, *von Wedel 1057* (GH, MO), *1314*, pro parte (GH, MO, US), *1340*, *1553*, *1754* (all GH, MO). Water Valley, *von Wedel 806* (MO), *1660*, pro parte (MO). CANAL ZONE: Barro Colorado Island, *Aviles 45* (F, MO); *Bailey & Bailey 655* (F); *Brown 12* (F); *Croat 4664* (MO), *4753* (MO, SCZ), *5226* (SCZ), *5406*, pro parte (MO), *6071* (MO, SCZ), *6088*, *6227*, *6843*, *7085*, *7126*, *7906*, *8209*, *8434*, *8704*, *11085*, *12846*, *15074* (all MO); *Foster 1308* (PMA); *Gentry 442* (MO, WIS), *1734* (MO); *Kenoyer 527* (US); *Shattuck 270* (A, F, MO), *512* (F, MO, US); *Wetmore & Abbe 28* (A, F), *28A* (A, MO); *Woodworth & Vestal 363* (A, F, MO, US). Chagres, *Fendler 206* (K, MO, US). COLÓN: W of Portobelo, *Gentry 1766* (MO). Río Indio de Fató, *Pittier 4258* (US). DARIÉN: Río Ucurgantí, *Bristan 1157*, pro parte (MO), *1169* (MO). Río Pirre, *Croat & Porter 15497* (MO). Río Balsas between Quebrado Chusomocater and Río Aretí, *Duke 8711* (MO). Río Jaqué to base of Cerro Pavarando, *Gentry 4199* (MO). Near mouth of Río Paya on Río

Tuira, *Gentry 4335* (MO). Río Tuira between Ríos Paya and Cube, *Gentry 4351* (MO). Río Tuira just above Río Cube, *Gentry 4369* (MO). Río Paya from Río Tuira to village of Paya, *Gentry 4381* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4401* (MO). Between Río Paya and Río Paca, *Gentry 4484* (MO). El Real, *Gentry 4577* (MO). Near Cerro Pirre on Río Parasenico, *Gentry 4688* (MO). PANAMÁ: Río Sulugandí from mouth to trail crossing, *Gentry 3743* (MO). SAN BLAS: Mainland opposite Playón Chico, *Gentry 6356* (MO). WITHOUT LOCALITY: *Bristan 196* (MO).

3. **Pachyptera parvifolia** A. Gentry, Phytologia 26: 448. 1973. TYPE: Colombia, Sur de Santander, *Haught 2179* (MO).

Vine, the branchlets subterete, the smallest striate and more or less angulate, inconspicuously capitate-puberulent or lepidote, glabrescent, the nodes without interpetiolar glandular fields; pseudostipules minute, less than 1 mm long, rhombic, acuminate, the margin much thinner when young. *Leaves* 2-foliolate, often with tendril; leaflets elliptic, rounded or emarginate to obtuse, small, to 3 cm long and 1.5 cm wide, membranaceous, basally asymmetrically rounded and more or less 3-nerved, the secondary veins obscure especially when young, conspicuously glandular-lepidote or lepidote-punctate, especially beneath, the glands larger and more crowded at the base; tendril simple, terminating in a woody, peltate disc, to 8 mm in diameter; petiolules 1–8 mm long, petiole 5–8 mm long, petiolules and petiole puberulous above. *Inflorescences* axillary to fallen leaves, short, ebracteate, 2–3-flowered, the peduncle 5–6 mm long, the pedicels 1.2–1.5 mm long, inconspicuously lepidote. *Flowers* with the calyx campanulate, truncate or shallowly bilabiate, the margin sometimes turned under, 5–6 mm long and 5–9 mm wide, inconspicuously lepidote or with a few scattered simple trichomes; corolla light purple or white, tubular-campanulate, 3.5–5 cm long and 0.8–1.2 cm wide at mouth, the base narrowed, the tube 2.5–4 cm long, the lobes 1–1.3 cm long, scurfy puberulous outside, mostly glabrous within, pubescent at the level of stamen insertion; stamens didynamous, the longer filaments 1.6–2.5 cm long, the shorter filaments 1.1–1.8 cm long, the anther thecae divaricate, 2–4 mm long, glabrous, the connective extended 0.5 mm, the staminode ca. 2 mm long, inserted 5–10 mm from the base of the corolla tube; pistil 2.8–2.9 cm long, the ovary oblong, subtetragonal, 3–4 mm long and 1 mm wide at the base, slightly wider at the top, densely and minutely lepidote, the ovules 4-seriate in each locule but appearing 2-seriate in most cross sections; disc almost spherical, 2 mm long and 3 mm wide. *Capsule* linear-oblong, woody, ca. 25 cm long and 2.5 cm wide, tan; seeds thin, the wings brownish, not sharply differentiated from the body.

The distinctive juvenile stage of this species has been collected a number of times from Honduras to Bolivia, but I have seen only two flowering collections, the type from Colombia and a specimen from Amazonian Brazil. It is apparently restricted to the tropical wet forest.

The juvenile stage is a tenuous vine with extremely small bifoliolate leaves, each bearing a short tendril terminated by a peltate disc. These plants grow closely appressed against the trunks of supporting trees, attached by the tendril-discs.

A note on the fruit of this species is in order. I collected fallen capsule

valves and seeds at two localities on the Río Brazo Viejo, Choco, Colombia, in an area where juvenile vines were common. The specimens were subsequently destroyed by the Summit Herbarium fire (June 1972) before measurement or critical examination. However, some previously planted seeds germinated, giving rise to the typical juvenile form and establishing the identity of the fruiting material with this species. My general impression of the fruit was that it was similar to that of *Ceratophytum* in size, color, and form, although much more compressed. Destruction of the collection prevents a more complete description.

Although inclusion of *P. parvifolia* in *Pachyptera* significantly enlarges the concept of the genus, it seems better than the alternative of erecting a new monotypic genus. This emphasizes the apparent affinities of the species rather than its peculiarities.

BOCAS DEL TORO: Water Valley, *von Wedel 687* (MO). Top of fila above Almirante, *Gentry 2769* (MO). DARIÉN: Between upper Río Membrillo and Camp 7 on the construction road to San Blas, 100–800 m, *Duke 10875* (MO).

4. **Pachyptera standleyi** (Steyermark) A. Gentry, Brittonia 25: 236. 1973.—FIG. 23F–I.

Pseudocalymma standleyi Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 235. 1947. TYPE: Guatemala, Quetzaltenango, *Steyermark 33533* (F).

P. alliaceum var. *macrocalyx* Sandw., Kew Bull. 1953: 468. 1954. TYPE: British Guiana, Demerara River, *Jenman 6752* (K, holotype; NY, isotype).

Liana to at least 5 cm in diameter, bark smooth, pale gray, the outer bark thin; stem with 8 phloem arms in cross section; all parts with strong garlic odor; branchlets subterete to subtetragonal, glabrous to scabridulous or inconspicuously lepidote, the nodes with interpetiolar glandular fields, the pseudostipules small, blunt-conical, with distinct upper and lower segments. *Leaves* 2-foliolate, sometimes with a tendril or tendril scar; leaflets elliptic, acute to short-acuminate, basally widely cuneate to rounded, 8.6–20 cm long and 3.7–22 cm wide, membranaceous, the secondary veins 7–10 on a side, glabrous or slightly lepidote especially at the base, beneath with glandular fields in axils of basal nerve pair; drying green to olive-green above and beneath; tendril trifid, 9–12 cm long to branching, the 3 arms 0.4–2.0 cm long; petiolules 0.7–2.0 cm long, petiole 0.9–3.2 cm long, glabrous or slightly lepidote as the petiolules, often with an apical glandular field. *Inflorescence* an axillary or terminal panicle (often reduced to a raceme), the branches glabrous or slightly lepidote, each flower subtended by 2 large, membranaceous, caducous, red-violet bracts, 0.8–1.9 by 0.6–1.1 cm. *Flowers* with odor of garlic, calyx thin, cupular, undulately 5-lobed, 9–21 mm long and 8–16 mm wide, mostly glabrous with raised glandular areas, red-violet when fresh; corolla rose-red on lobes and upper tube outside, the base of the tube yellow inside and out, upper tube within yellow with pinkish hue; tubular-campanulate above a 1.5 cm by 0.4 cm tubular base, 3.8–8.4 cm long and 0.8–1.9 cm wide at the mouth, the tube 3.5–6.0 cm long, the lobes 0.6–2.7 cm long; the tube glabrous inside and out except for multicellular, partially gland-tipped simple trichomes inside at the level of

stamen insertion, the lobes simple-puberulous; stamens didynamous, the abaxial pair often exserted, the anther thecae straight, divaricate, 3–4 mm long, the longer filaments 2.4–3.0 cm long, shorter filaments 1.1–2.2 cm long, the staminode 1–2 mm long, inserted 11–16 mm from the base of corolla tube; pistil 4.2–4.9 cm long, the ovary linear-cylindric, 5 mm long and 1 mm wide, pustular-lepidote, the ovules 2-seriate; disc annular-pulvinate, 1 mm long and 4 mm wide. *Capsule* (including extralimital material) elongate-linear, flat, acute at both ends, drying tan, glabrous but more or less punctate, the median nerve not visible, 35–75 cm long and 2.6–3.8 cm wide; seeds thin, bialate, 2–2.8 cm long and 7.5–11 cm wide, the wings pale white, subhyaline, poorly demarcated.

A plant of the tropical wet forest and wetter parts of the tropical moist forest, this species ranges from Guatemala to Venezuela and Peru. It evidently flowers somewhat sporadically, having been collected in flower twice in April and once in September.

This species has been confused with *P. hymenaea* (DC.) A. Gentry and *P. alliacea* (Lam.) A. Gentry but is both morphologically and ecologically distinct.

BOCAS DEL TORO: Daytonia Farm, *Cooper 450* (F). Western River, *von Wedel 2700* (GH, MO, US). CHIRIQUÍ: Burica Peninsula near Punta de Piedra, *Croat 22447A* (MO). PANAMÁ: Archaeological site near Madden Lake, *Gentry & Tyson 5027* (MO, SCZ).

24. PARAGONIA

Paragonia Bur., Bull. Soc. Bot. France 19: 17. 1872. TYPE: *Bignonia lenta* Mart. *ex* DC. = *Paragonia pyramidata* (L. C. Rich.) Bur.

Lianas; stems with 4 phloem arms in cross section; branchlets terete, lenticellate, interpetiolar glands lacking or rare; pseudostipules subconical, basally thick and pointed at the tip with the inner side appressed against the twig. *Leaves* 2-foliolate, often with a minutely bifid, rarely minutely trifid, tendril, the petiole with a glandular field on the upper side near the apex. *Inflorescence* a large, terminal, many-flowered panicle. *Flowers* with the calyx more or less cupular, truncate to somewhat lobed, lepidote, usually ciliate; corolla pale lavender to magenta, tubular-campanulate, velvety moniliform-pubescent outside; anthers glabrous, the thecae straight, divaricate; pollen grains single, 3-colpate, the exine almost smooth; ovary narrowly cylindric, the walls relatively thick, lepidote, the ovules 2-seriate in each locule. *Fruit* an elongate-linear capsule, the valves convex, finely tuberculate with the texture of coarse sandpaper; seeds thin, bialate, the wings chocolate brown, not demarcated from seed body.

One species of continental tropical America ranging from Mexico to Argentina; also reported on Guadeloupe.

1. **Paragonia pyramidata** (L. C. Rich.) Bur., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 104. 1894.—FIG. 24.

Bignonia pyramidata L. C. Rich., Act. Soc. Hist. Nat. Paris 1: 110. 1792. TYPE: French Guiana, *LeBlond 292* (P-LA).

B. laurifolia Vahl, Eclog. Amer. 2: 44. 1798. TYPE: Trinidad, *van Rohr s.n.* (C).
B. ehretioides Cham., Linnaea 7: 704. 1832. TYPE: Brazil, *Sellow s.n.* (fide Kunth, Fedde Rep. Beih. 43: 635. 1928; not seen).
B. striata DC., Rev. Bign. (Bibl. Univ. Genève) 22. 1838, nomen nudum.
B. rupestris Gardn., Jour. Bot. (Hooker) 1: 179. 1842. TYPE: Brazil, Rio de Janeiro, *Gardner 78* (K).
B. sinclairii Benth., Bot. Voy. Sulphur 129. 1844. TYPE: Panama, *Sinclair s.n.* (K).
Zeyheria? surinamensis Miq., Linnaea 18: 250. 1844. LECTOTYPE: Surinam, *Focke 230* (U, holotype, excluding leaves of *Cydista aequinoctialis*; K, isotype).
Bignonia lenta Mart. *ex* DC., Prodr. 9: 159. 1845. TYPE: Brazil, Amazonas, *Martius 2977* (M; G-DC, fragments).
B. martiusiana DC., Prodr. 9: 156. 1845. TYPE: Brazil, Para, *Martius s.n.* (1817) (BR).
Pachyptera dasyantha DC., Prodr. 9: 176. 1845. TYPE: Brazil, Rio São Francisco, *Blanchet 2903* (G-DC, K).
P. perrottetii DC., Prodr. 9: 176. 1845. TYPE: French Guiana, *Perrottet 2851* (G-DC).
Pachyptera striata DC., Prodr. 9: 176. 1845. TYPE: Brazil, São Paulo, *Lund 783* (G-DC).
P. umbelliformis DC., Prodr. 9: 186. 1845. SYNTYPES: Brazil, São Paulo, *Martius s.n.* (M, not seen); Rio Paraiba, *Neuwied s.n.* (M, not seen).
Pithecoctenium reticulare DC., Prodr. 9: 197. 1845. TYPE: Brazil, without data (G-DC, fragment).
Tabebuia pyramidata (L. C. Rich.) DC., Prodr. 9: 214. 1845.
Temnocydia elliptica Mart. *ex* DC., Prodr. 9: 156. 1845, pro syn.
T. lenta Mart. *ex* DC., Prodr. 9: 159. 1845, pro syn.
Arrabidaea dichasia Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 6. 1895. TYPE: Honduras, Santa Barbara, *Thieme 5393* (NY, US).
Adenocalymma densiflora Rusby, Descr. 300 New Sp. S. Amer. Pl. 122. 1920. TYPE: Bolivia, Cataracts of Bopi River, *Rusby 484* (NY, US).
Petastoma leiophyllum Kränzl., Fedde Repert. 17: 58. 1921. TYPE: Brazil, Parana, *Dusén 8633* (K).
P. macrocalyx Kränzl., Fedde Repert. 17: 59. 1921. TYPE: Brazil, São Paulo, *Heiner 569* (S, not seen; K, photo).

Liana with somewhat swollen nodes, to 5 cm in diameter, the grayish bark usually thick and soft-corky ridged, the ridges sometimes flattened and obsolescent; stem with 4 phloem arms in cross section; branchlets terete with raised, warty lenticels, somewhat lepidote, sometimes slightly puberulous when young especially at the nodes, interpetiolar glands mostly lacking, an interpetiolar ridge often present; pseudostipules present, of 2–3 scales, basally thick and pointed apically with the inner side appressed against the twig. *Leaves* 2-foliolate, sometimes with a tendril (rarely incompletely 3-foliolate); leaflets elliptic to elliptic-obovate or elliptic-ovate, acute, cuneate to rounded, 6.9–22 cm long and 2.3–12.5 cm wide, membranaceous to chartaceous, secondary veins (3–)4–6 on a wide, strongly ascending, generally lauraceous in appearance, sometimes puberulous on the midvein beneath, lepidote above and beneath, a few plate-shaped glands scattered near the midvein beneath, the main veins often whitish when fresh, usually a uniform gray or olive when dry, when fresh with a sweet smell when crushed; tendril simple or bifid, rarely trifid, at the extreme tip, 5–17 cm long; petiolules 0.7–4.7 cm long, petiole 0.9–4.5 cm long, above with an apical glandular field, lepidote to puberulous. *Inflorescence* a many-flowered terminal panicle, the branches lepidote to puberulous. *Flowers* with a sweet slightly spicy aroma, calyx cupular, irregularly truncate to somewhat bilabiate, lepidote, usually ciliate around the mouth with simple trichomes, (3–)4–7 mm long, 4–10 mm wide; corolla pale lavender to magenta, inside with the top and base of the tube white, tubular-campanulate, 2.7–5.5 cm

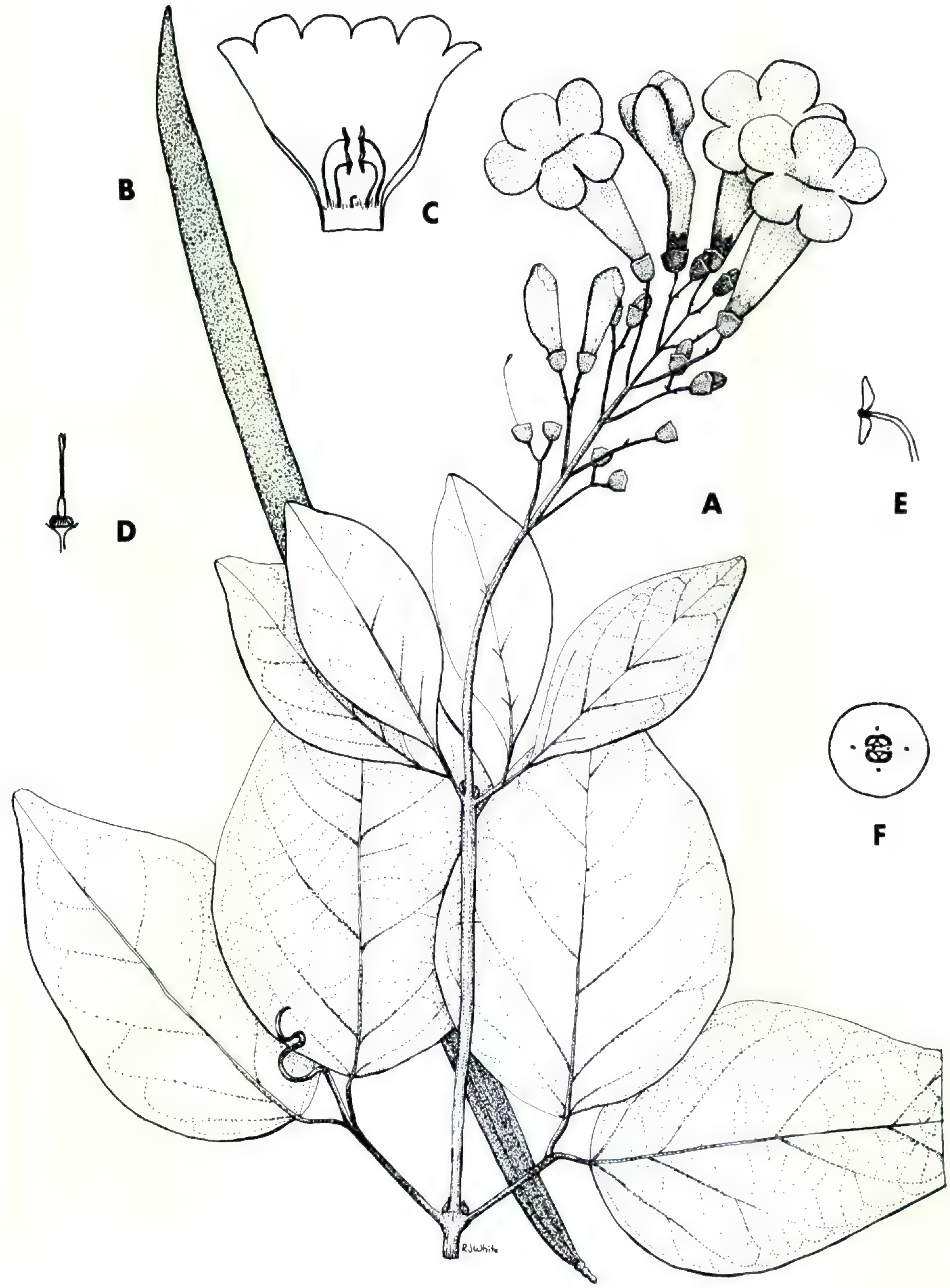


FIGURE 24. *Paragonia pyramidata* (L. Rich.) Bur.—A. Habit (× ½). [After *Gentry 2903* (MO).]—B. Fruit (× ½). [After *Croat 5641* (MO).]—C. Corolla split open (× ½). —D. Pistil and disc (× ½).—E. Anther (× 2).—F. Ovary cross section (× 8½). [After *Gentry 1789* (MO).]

long and 0.8–2.2 cm wide at the mouth, the tube 2.1–4.0 cm long, the base somewhat thickened, the lobes 0.5–1.5 cm long, thickly simple-pubescent with moniliform trichomes outside and on the lobes inside, the tube mostly glabrous inside, densely simple-pubescent with long multi-cellular, jointed trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2–2.5 mm long, the filaments slightly short-puberulous near the base with a conspicuous tuft of long, jointed trichomes at the extreme base, the longer pair 1.6–1.9 cm long, the shorter pair 1.2–1.5 cm long, the staminode 4–6 mm long, inserted 3–5 mm from the base of the corolla tube; pistil 1.9–2.0 cm long, the ovary linear, 4–5 mm long and 1.5 mm wide, strongly lepidote, the ovules 2-seriate; disc annular-pulvinate, 1.5–2.0 mm long and 4 mm wide. *Capsule* linear, tapering at the ends, not strongly flattened, the valves convex, 32–61 cm long and 1.2–1.4 cm wide, to 0.7 cm thick, surface finely tuberculate, resembling coarse sandpaper in texture; seeds 0.8–1.2 cm long and 2.1–4.4 cm wide, the wings membranaceous, chocolate-brown, not sharply demarcated from the seed body.

An abundant liana of the tropical wet forest and premontane wet forest, *P. pyramidata* is also common in the tropical moist forest. Ecologically it is equally well adapted to well-drained hillsides or swamps. It ranges from Mexico to Brazil and Bolivia. This species flowers erratically throughout the year but mostly during the dry season.

Distinguishing characteristics include the sweet smell of the broken leaves, the typical pseudostipules, and the large lauraceous-looking leaflets. Vegetatively it is most easily confused with *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw., which has similar leaves and pseudostipules but also conspicuous interpetiolar glands and trifid tendrils. *Paragonia* lacks interpetiolar glandular fields and has simple or minutely bifid tendrils.

BOCAS DEL TORO: Changuinola on Río Changuinola, *Dwyer 2892* (MO). Hillside above Almirante, *Gentry 2694* (MO). Vicinity of Chiriquí Lagoon, *von Wedel 1345*, pro parte (GH, MO). Fish Creek Lowlands, *von Wedel 2377* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Brown 186* (F); *Croat 4762, 4805* (both MO, NY, SCZ), *4917* (MO, SCZ), *5591* (MO, NY, SCZ), *5615* (MO), *5641* (MO, NY), *5645* (MO, SCZ), *5705* (NY, SCZ), *6538* (MO, NY, SCZ), *6584, 7131* (both MO), *7695* (MO, NY, SCZ), *7744, 7895* (both MO), *7896* (MO, SCZ), *8136, 8309A, 8370, 9106, 9227, 9510* (all MO), *10161* (MO, SCZ), *10212* (MO), *10358* (MO, SCZ), *11932, 14626, 14940* (all MO); *Foster 689, 1090* (both PMA); *Gentry 430* (MO, WIS), *433, 451, 719* (all MO); *Standley 40941* (US); *Starry 150* (F, MO); *Wetmore & Abbe 210* (F); *Wetmore & Woodworth 1* (F), *847* (A); *Woodworth & Vestal 454* (A, F, MO), *576* (A, F). Near mouth of Río Chagres, *Allen 898* (K, MO, NY, US). Matachin, *Cowell 193* (NY). Pipeline Road, *Gentry 1417, 1580* (both MO). Road K-19, *Gentry 1789* (MO). Pipeline Road, *Gentry 1899, 2459* (both MO). Panama Station, Panama Railroad, *Hayes 413* (BM). Río Gatún, *Hayes 915, 1043* (both NY). Las Cruces trail crossing in Madden Forest, *Harvey 5285* (F). Gamboa road, *Jones 306* (US). Banks of Chagres River below Gatún, *Maxon 4795* (BM, NY, US). Near Cruces, *Seemann 400* (K). Chilibre River to 1 mi. below Chilibre, *Seibert 1513* (US). CHIRIQUÍ: W of Río Chorchita, *Gentry 5849* (MO). COCLÉ: El Valle de Antón, *Allen 1751* (F, GH, MO, NY, US); *Alston 8715* (BM); *Gentry & Dwyer 3572* (MO). Bismark above Penonomé, *Williams 263* (NY, US). COLÓN: Río Gatuncillo in vicinity of Santa Rosa, *Allen 4166* (MO). W of Portobelo, *Gentry 1764* (MO). DARIÉN: Río Ucurgantí, *Bristan 1157*, pro parte (MO). Santa Fé, *Duke 14251* (K, MO). Río Aretí, *Duke & Nickerson 14910* (MO). Vicinity of Jaqué, *Gentry 4109, 4183, 4187* (all MO). Cerro Chucula, drainage of Río Pavarando, *Gentry 4258* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4406* (MO). El Real, *Gentry 4501* (MO). Near

Cerro Pirre on Río Parasenico, *Gentry 4690* (MO). Near mouth of Pavarandó on Sambú River, *Pittier 5577* (US). HERRERA: S of Ocú, *Gentry 3129* (MO). LOS SANTOS: Vicinity of Tonosí, *Stern et al. 1875* (MO, US); *Tyson et al. 2941* (MO, SCZ), *3102* (MO, PMA). PANAMÁ: Lagarto Bay (Río Maestro?), *Barclay 2777* (BM). Cerro Campana, *Gentry 1835* (MO). Río Maestro, *Gentry 2210* (MO). Río Pasiga, *Gentry 2311* (MO). Río Piragua (Tabardí), *Gentry 2527* (MO). Río Piragua above confluence with Río Bayano, *Gentry 2588* (MO). Río Corona, *Gentry 2903* (MO). Near Río Espavé, *Gentry 3710* (MO). Trail from Río Espavé toward Río Agua Clara, *Gentry 3759* (MO). Along Río Bayano just above mouth of Río Espavé, *Gentry 3782* (MO). Near last river before Río Partí on trail from Río Bayano, *Gentry 3801* (MO). Near Madden Lake, *Gentry 5002* (MO). Río Chamé, *Moran 29* (PMA). SAN BLAS: Near Puerto Obaldía, *Gentry 1444* (MO). Mainland opposite Playón Chico, *Gentry 6384* (MO). Ailigandi River, *Lewis et al. 171* (MO, SCZ). VERAGUAS: Vicinity of Santa Fé, *Gentry 2942, 3030* (both MO). WITHOUT LOCALITY, *Cuming 1179* (BM); *Sinclair s.n.* (K).

25. PARMENTIERA

Parmentiera DC., Rev. Bign. (Bibl. Univ. Genève) 19. 1838. TYPE: *P. edulis* DC. = *P. aculeata* (H.B.K.) Seem.

Zenkeria Reichb., Nom. 236. 1841, fide *Index Kewensis*.

Shrubs to quite large *trees*; often armed with a spine below each node. *Leaves* opposite or subopposite, mostly palmately 3–5-foliolate, often with a slightly winged petiole. *Inflorescence* a single flower or fascicle of 2–3 flowers, usually borne cauliflorously on the old wood or trunk, sometimes terminally. *Flowers* with the calyx spathaceous, split ventrally to near its base, inconspicuously lepidote; corolla white or greenish-white, large, broadly campanulate to infundibuliform, usually with a transverse fold across the lower side of the throat; stamens subexserted, anthers glabrous, the thecae thick, straight, somewhat divergent; pollen grains 3-colpate, the exine finely granular; ovary cylindrical, the epidermis glandular and appearing more or less lepidote when dry, the ovules multiseriate; disc annular-pulvinate. *Fruit* elongate-linear to oblong, indehiscent, often longitudinally ridged, with a firm, fleshy outer cortex and a fibrous-fleshy core; seeds between cortex and core, small, flattened, encircled by a narrow vestigial wing.

Eight species of Central America ranging from southern Mexico to Colombia.

a. Small trees, the branchlets usually with 2 short incurved spines at most nodes; fruit thick, conspicuously costate and curved, less than 17 cm long; cultivated ..... 1. *P. aculeata*
aa. Small to large trees, the branchlets without spines; fruit slender or thick, cylindric, not conspicuously curved, more than 30 cm long; native but also cultivated.
  b. Shrubby trees, usually several-branched near the base; petiole winged; fruits slender, less than 2.4 cm wide, even when fresh, terete, not ribbed; moist forest, central Panama and in cultivation ..... 2. *P. cereifera*
  bb. Erect trees or treelets, branched only in the crown; petiole unwinged (except in seedlings); fruits cylindrical, thick, more than 4 cm wide when fresh, suboctagonal in cross section, conspicuously ribbed; wet forest, central and western Panama ..... 3. *P. macrophylla*

1. **Parmentiera aculeata** (H.B.K.) Seem. Bot. Voy. Herald 183. 1854.

Crescentia edulis Desv., Jour. Bot. (Desvaux) 4: 112. 1814. TYPE: (not seen; not *Parmentiera edulis* DC.).

C. aculeata H.B.K., Nov. Gen. Sp. Pl. 3: 158. 1819. TYPE: Mexico, Campeche, *Bonpland s.n.* (P.).
C. edulis Moc. *ex* DC., Prodr. 9: 244. 1845, pro syn., non Desv.
Parmentiera edulis DC., Prodr. 9: 244. 1845. TYPE: Mexico, based on a Sessé and Mociño drawing (not seen).
Crescentia musaecarpa Zaldivar *ex* Heller, Reisen in Mexico 414. TYPE: Mexico (not seen).
Parmentiera foliolosa Miers, Trans. Linn. Soc. 26: 166. 1870. TYPE: Mexico, *Schiede 1207* (K).
P. lanceolata Miers, Trans. Linn. Soc. London 26: 167. 1870. TYPE: Based on *Crescentia edulis* Desv.

Small *tree*, branchlets terete, the nodes armed with a thick thorn subtending each leaf, the leaves opposite or subopposite, mostly 3-foliolate, a few simple, the leaflets elliptic-obovate, acute to obtuse, the base cuneate or attenuate, terminal leaflet 3.4–4.7 cm long, lateral leaflets 2.1–4.7 cm long, with barbate chambers in the nerve axils beneath; petiolules lacking, petiole 1.3–3.5 cm long, strongly grooved on top but not winged. *Inflorescence* a few-flowered fascicle or reduced to a single flower, terminal or axillary near the branch tips, or from nodes of old wood. *Flowers* with the calyx basically spathaceous, sometimes additionally split, ca. 3 cm long; corolla white, campanulate, 5–6 cm long and 2–2.5 cm wide at the mouth; stamens subexserted, the anther thecae somewhat divergent, thick, ovary oblong-linear, lepidote, the ovules multiseriate in each locule. *Fruit* to 17 cm long, more than 3 cm in diameter when fresh, curved, costate with thick ribs.

No collections have been seen from Panama and the above description is taken from Mexican material. Native to southern Mexico and northern Central America, the species is occasionally cultivated outside its range. Reported by Standley as cultivated in lowland Costa Rica, it is probably cultivated sporadically in Panama. It is readily distinguished from the native species by its axillary spines.

2. **Parmentiera cereifera** Seem. *in* Hook., Jour. Bot. (Hooker) 3: 302. 1841. TYPE: Panama: Río Chagres, *Seemann s.n.* (K).—FIG. 25A–E.

Small *tree* to 20 cm d.b.h. and 7 m tall, usually several-branched near the base, the main branches strongly ascending, the crown open; twigs terete, subpuberulous, the nodes often double with a pair of small leaves in the axil of a larger pair, foliaceous pseudostipules sometimes present, 6–10 mm long and 3–4 mm wide. *Leaves* opposite, 3-foliolate; leaflets elliptic to elliptic-rhomboid, acute to acuminate, basally attenuate, the terminal leaflet 3.6–9.5 cm long and 1.4–4 cm wide, the lateral leaflets 3.0–6.5 cm long and 1.4–3.6 cm wide, membranaceous, secondary veins in 4–6 pairs, somewhat lepidote at least beneath, simple-puberulous along the midvein above and beneath, especially in axils of lateral nerves, usually with a few plate-shaped glands along the mid-vein beneath, drying olive to blackish; petiolules not differentiated, petiole conspicuously winged, 2.4–6.2 cm long, the wing to 0.4 cm wide, widest apically and basally attenuate, the midrib slightly scabrous. *Inflorescence* a single cauliflorous flower or a fascicle of 2–3 flowers borne on abbreviated short-shoots on larger branches or trunk, the pedicels lepidote, 0.9–1.6 cm long.

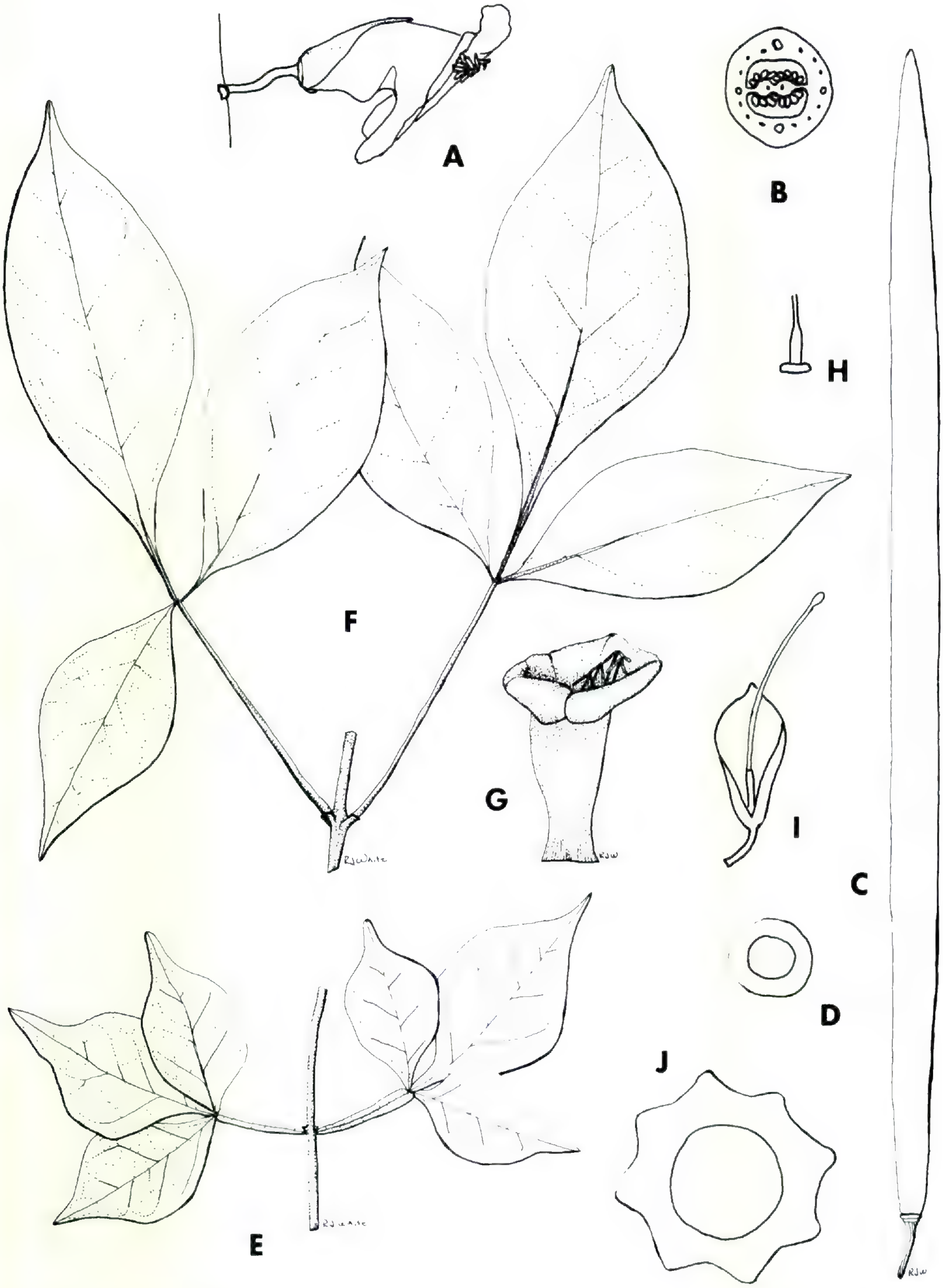


FIGURE 25. *Parmentiera*.—A–E. *P. cereifera* Seem.—A. Inflorescence (× ½).—B. Ovary cross section (× 9).—C. Fruit (× ⅜).—D. Fruit cross section (× ½).—E. Leaves (× ½). [After *Gentry 5610* (MO).]—F–J. *P. macrophylla* Standl.—F. Leaves (× ½).—G. Corolla (× ½).—H. Ovary and disc (× ¾).—I. Calyx (× ½).—J. Fruit cross section (× ½). [After *Gentry 754* (MO).]

Flowers with musky odor, the calyx spathaceously split on the ventral side, 1.9–4.9 cm long and 0.9–2.9 cm wide, inconspicuously lepidote, at least at the base; corolla pure white, tubular with a horizontal pleat midway across the lower side of throat, slightly fleshy, 3.7–6.4 cm long and 1.8–2.9 cm wide at the mouth, the tube 2.5–4.0 cm long, the lobes basally fused, 1.0–1.1 cm long, mostly glabrous throughout, the epidermal cells apparently glandular, a few stalked-lepidote trichomes at the level of stamen insertion inside and on lobes outside; stamens subexserted, the anther thecae thick, partially divergent, 5–8 mm long, the anterior filaments 2.6–3.5 cm long, inserted 1.1–1.8 cm from base of corolla tube, the posterior filaments 2.7–3.2 cm long, inserted 1.2–1.7 cm from the base of the corolla tube, the staminode 1.0–1.9 cm long, inserted 0.9–2.3 cm from the base of corolla tube; pistil 3.1–4.8 cm long, the ovary linear-cylindrical, 7–8 mm long and 1.5–2 mm wide, glabrous with glandular epidermis, the ovules irregularly 8–10-seriate; disc annular-pulvinate, 1.5–2 mm long and 6 mm wide. *Fruit* elongate-linear, subterete in cross section, 39–54 cm long and 1.0–2.4 cm wide, glabrous to sparsely lepidote, waxy yellow, divided into a fleshy part surrounding the seeds and a fibrous central core surrounded by the seeds; seeds small, thin, 3–4 cm long and 3–4 cm wide, with a narrow but distinct mucilaginous wing.

A locally common small to medium-sized tree, *P. cereifera* is apparently restricted in nature to the tropical moist forest of the Atlantic slope of Central Panama. It is widely cultivated as a curiosity throughout the tropics. Flowering throughout the year, it is pollinated by bats. The flowers do not open until 4:00 or 5:00 in the evening. Fruit set is abundant and the waxy-fleshy fruits fall beneath the parent tree at maturity. The fruit pulp is relished by a number of mammals. According to Standley (Contr. U. S. Natl. Herb. 27. 1928) it is an important food for cattle in some parts of Panama. Dispersal of the small, slippery, slime-coated seeds is probably effected by mammals which eat the fruit. The common names "palo de velas" or "candle tree" refer to the candle-like appearance of the fruit.

The elongate-fleshy fruits of *Parmentiera* separate it from other Crescentieae. The compound leaves of *Parmentiera* are opposite in contrast to the likewise 3-foliolate but fasciculate leaves of *Crescentia alata*. *Parmentiera cereifera* is distinguishable from other species of the genus by its tendency to divided trunks and its narrower fruits. It is the only native Crescentieae of the non-coastal tropical moist forest.

CANAL ZONE: Summit Garden, *Correa et al. 1689* (PMA). Near Salamanca Hydrographic Station in gorge of Río Pequení, *Dodge et al. 16963* (MO). Boy Scout road near Madden Lake, *Gentry 2053, 2488, 5060* (all MO). Barbacoa, *Hayes s.n.* (BM). Matachin, *Hayes 604* (NY). Dirt road near parking area for Madden Dam, *Kirkbride & Elias 267* (NY, SCZ). Vicinity of Madden Dam, *Lewis et al. 21* (GH, MO, US). Vicinity of Gatuncillo, *Piper 5611, 5641, 6009* (all US). Between Gorgona and Mamei, *Pittier 2237* (BM, C, NY, US). Río Chagres, *Seemann s.n.* (K). Chilibre River below Chilibre, *Seibert 1503* (MO, US). Río Pedro Miguel near E Paráiso *Standley 29979* (US). Vicinity of Fort Sherman, *Standley 31132* (MO, US). Mamei and Gorgona, *Wagoner 35* (M). Madden Dam, *Woodson et al. 1554* (A, MO, NY). Vicinity of Salamanca Hydrographic Station on Río Pequení, *Woodson et al. 1607* (A, MO, NY). Without locality, *Gaillard s.n.* (US), *Gaillard s.n.* (NY, US); *Johansen 16* (US).

3. **Parmentiera macrophylla** Standl., Publ. Field Columbian Mus., Bot. Ser. 4: 263. 1929.—TYPE: Panama, Bocas del Toro, *Cooper 402* (F, K, US).—FIG. 25F–J.

P. macrophylla Standl., Trop. Woods 16: 12. 1928, nomen nudum.

Small to medium-sized *tree* to 30 cm d.b.h. and 25 m tall, the trunk usually erect and unbranched for much of its length, the crown open; twigs terete, glabrous to slightly and inconspicuously scabridulous. *Leaves* mostly opposite, sometimes subalternate, often ± fasciculate, 3-foliolate; leaflets rhomboid-elliptic, acuminate to acute, basally attenuate, the terminal leaflet 6.8–13.2 cm long and 2.6–5.9 cm wide, the lateral leaflets 4.7–10.7 cm long and 1.8–4.9 cm wide, membranaceous, secondary veins 5–7 on a side, somewhat lepidote or deciduous-lepidote, especially beneath, otherwise glabrous except for a ciliate fringe of short simple trichomes along the margins, well-developed chambers at the vein axils beneath, usually with a few plate-shaped glands along the midvein beneath, drying dark olive above, pale olive beneath; petiolules winged but usually differentiated from the decurrent leaflet bases, the terminal petiolule to 3.5 cm long, the lateral petiolules to 1.1 cm long, the petiole unwinged except on immature plants, furrowed above, glabrous, 3.6–7.2 cm long. *Inflorescence* of one or 2 flowers borne along the trunk, the pedicels lepidote. *Flowers* with a musky odor, calyx spathaceously split and ventral side, 2.6–5.0 cm long and 0.8–1.2 cm wide, basally lepidote, otherwise mostly glabrous with a conspicuously glandular epidermis when fresh; corolla pure white with a faint greenish tinge outside; tubular-campanulate with an inconspicuous saccate bulge in the floor of the throat, fleshy, 4.9–6.3 cm long and 1.5–2.5 cm wide at the mouth, the tube 3.6–4.5 cm long, the 3 lower lobes 0.8–1.0 cm long, the upper 2 fused half their length; glabrous throughout except for a few glandular-lepidote enations at the level of stamen insertion, the epidermis conspicuously glandular; stamens subexserted, the anther thecae thick, 1.5–2.0 mm wide, partially divergent, 5–6 mm long, the anterior filaments 3.3–3.8 cm long, inserted 1.5–1.7 cm from the base of the tube, the posterior filaments 3.3–3.8 cm long, inserted 1.7–2.1 cm from the base of the tube, the staminode 4–16 mm long, sometimes totally fused to the corolla tube; pistil 5.7–5.9 cm long, the ovary narrowly cylindric, octagonal in cross section, 6–7 mm long and 2 mm wide, glabrous with a glandular epidermis, the ovules ± 6-seriate; disc annular pulvinate, 1.5 mm long and 5 mm wide. *Fruit* cylindric with conspicuous longitudinal ribs, suboctagonal in cross section, 44–50 cm long and ca. 6 cm wide when fresh and 2.8 cm wide when dried, waxy yellow when fresh, drying black, divided into a fleshy part outside the seeds and a fibrous core inside the seeds; seeds small, thin, 3–6 cm long and 8–9 cm wide, with a distinct, narrow mucilaginous wing when fresh.

A tree typical of wet upland areas, *P. macrophylla* is found in wet forest and lower montane rain forest, mostly at elevations above 500 meters. It is known only from Costa Rica and Panama. It flowers irregularly through most

of the year especially during the wet season. The fleshy fruit is eaten by mammals.

Parmentiera macrophylla is quite variable in habit and ranges from a straight-trunked tree, 30 cm in diameter and 25 m tall, to sexually mature saplings, only 2.5 cm thick and 3 m tall. It is separated from *Parmentiera cereifera* by its different ecological requirements, its much thicker, longitudinally-ridged fruit, and at maturity by its unwinged petiole. *Parmentiera trunciflora* Standl. & L. O. Wms. of Nicaragua is perhaps a form of *P. macrophylla*.

BOCAS DEL TORO: Region of Almirante, *Cooper 402* (F, K, US). Chinguinola Valley, Island Potrero, *Dunlap 421* (F). Above Almirante, *Gentry 2802, 2815* (both MO). Vicinity of Chiriquí Lagoon, *von Wedel 1101* (GH, MO). Water Valley, *von Wedel 1421* (GH, MO, US). Darkland, *von Wedel 2619* (GH, MO, NY, US). COCLÉ: N rim of El Valle de Antón, *Allen 1782* (F, GH, MO, NY, US); *Duke 12174* (MO); *Dwyer et al. 4550* (MO); *Gentry & Dwyer 3663, 3658* (both MO); *Hunter & Allen 307* (MO); *Kirkbride 1089*; *Lewis et al. 1780* (MO); *Luteyn 1214* (MO).

26. PHRYGANOCYDIA

Phryganocydia Mart. *ex* Bur., Bull. Soc. Bot. France 19: 18. 1872. TYPE: *P. corymbosa* (Vent.) Bur.

Phrygiobureaua O. Kuntze *in* Post & Kuntze, Lexic. 433. 1903.

Lianas; stems with 8 (sometimes 4) phloem arms in cross section; branchlets terete without interpetiolar glandular fields at the nodes; pseudostipules inconspicuous or lacking, sometimes thick-foliaceous but early caducous on young twigs. *Leaves* simple or bifoliolate, often with a simple tendril, more or less lepidote but otherwise glabrous. *Inflorescence* a few-branched bifurcating panicle, sometimes reduced to a single flower. *Flowers* with the calyx spathaceously split to below the middle, thin, the narrowing tip more or less reflexed; corolla lavender to magenta, tubular-infundibuliform, lepidote outside; anthers glabrous, the thecae straight, divaricate; pollen grains ecolpate, the exine finely reticulate; ovary rounded-conical to narrowly cylindrical, lepidote, the ovules 2-seriate in each locule; disc lacking. *Fruit* a capsule, the valves parallel to the septum, the surface densely lepidote, smooth but microscopically crystalline-rough, the median nerve indistinct; the capsule compressed and linear-oblong with thin brown-winged, bialate seeds or short, ovid, and slightly compressed with thick, corky wingless seeds.

Three species of continental tropical America ranging from Costa Rica to Brazil and Bolivia. *Phryganocydia* can be recognized in flower by its spathaceous calyx.

a. Leaves simple or 2-foliolate, coriaceous, the blades ovate, long-acuminate; capsule ovoid (more than 3.7 cm wide), slightly compressed, appearing yellowish, the seeds thick, corky, wingless, less than 3.5 cm wide; mangrove swamps and their fringes, Pacific coast ..... 2. *P. phellosperma*

aa. Leaves 2-foliolate, chartaceous, the blades elliptic to elliptic-ovate, acute or short-acuminate; capsule linear-oblong (less than 2.3 cm wide), strongly compressed, appearing grayish, the seeds thin, winged, more than 4.7 cm wide; well-drained sites, central and eastern Panama ..... 1. *P. corymbosa*

1. **Phryganocydia corymbosa** (Vent.) Bur. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 224, *fig.* 89*H*. 1894.—FIG. 26C–D.

Spathodea corymbosa Vent., Choix *tab. 40*. 1807; Mém. Math. Phys. Inst. Natl. France 1: 1–20. 1807. TYPE: Trinidad, *Riedlé s.n.* (P).
S. laurifolia H.B.K., Nov. Gen. Sp. Pl. 3: 114. 1819. TYPE: Venezuela, Sucre, *Humboldt & Bonpland s.n.* (P).
S. orinocensis H.B.K., Nov. Gen. Sp. Pl. 3: 147. 1819. TYPE: Venezuela, Orinoco, *Humboldt & Bonpland s.n.* (P).
Bignonia coito Vell., Fl. Flum. 244. 1825; 6: *tab. 19*. 1827. TYPE: Brazil (not seen).
Spathodea coito (Vell.) DC., Prodr. 9: 204. 1845.
Phryganocydia dipleuropus Mart. *ex* DC., Prodr. 9: 204. 1845, pro syn. TYPE: Brazil, Para, *Martius s.n.* (BR, M).
Spathodea platypoda DC., Prodr. 9: 204. 1845. TYPE: Brazil, Bahia, *Blanchet 1511* (G-DC, P).
Macfadyena corymbosa (Vent.) Griseb., Bonplandia 6: 10. 1858.
M. coito (Vell.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
M. laurifolia (H.B.K.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
M. lepidota Seem. *ex* Miers, Proc. Roy. Hort. Soc. 3: 200. 1863, nomen nudum. TYPE: West Indies (*sic*), *Shakespear s.n.* (drawing by Miers at P).
M. amazonica Miers, Proc. Roy. Hort. Soc. 3: 200. 1863, nomen nudum. TYPE: Brazil, Santarem, *Spruce s.n.* (P).
M. orinocensis (H.B.K.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
M. ovata Miers, Proc. Roy. Hort. Soc. 3: 200. 1863, nomen nudum. TYPE: Colombia, *Cuming 1118* (P).
M. platypoda (DC.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863.
Phryganocydia coito (Vell.) Bur. *ex* Baill., Hist. Pl. 10: 35. 1888.
Macfadyena bangii Rusby, Bull. Torrey Bot. Club 27: 72. 1900. TYPE: Bolivia, junction of Beni and Madre de Dios Rivers, *Rusby 1139* (NY, US).
Phryganocydia orinocensis (H.B.K.) Schnee *in* Pittier et al., Cat. Fl. Venez. 2: 401. 1947.

Liana to 5 cm in diameter, the bark smooth and fibrous to noticeably rough-lenticellate; stem with 8 phloem arms in cross section; branchlets subterete, finely longitudinally striate, lenticels inconspicuous, lepidote to glabrous, interpetiolar glandular fields lacking; pseudostipules usually inconspicuous or lacking, occasionally thickly foliaceous, but small and soon deciduous on young twigs. *Leaves* 2-foliolate, sometimes with a tendril; leaflets elliptic to ovate-elliptic, basally mostly acute, acuminate, or rounded, 4.1–22 cm long and 1.9–11 cm wide, chartaceous to subcoriaceous, secondary veins (3–)4–7(–8) on a side, often 3-veined from the base, densely minute-lepidote beneath, less so above, otherwise glabrous, olive to gray-brown when dry, the midvein often reddish-brown beneath; tendril simple, 7–16 cm long; petiolules 0.5–3.0 cm long, usually slightly winged, petiole 0.6–3.3 cm long, strongly lepidote. *Inflorescence* a small axillary or terminal panicle, the branches lepidote, somewhat enlarged and often flattened at articulations. *Flowers* somewhat sweet-smelling, calyx spathaceously split from near the tip to 1 cm from the base, the long narrowing tip curved away from the corolla, apically blunt lepidote, 2.1–4.1 cm long to the tip and 0.6–1.4 cm wide at widest point; corolla lavender with a white throat and magenta spot at the base of the upper corolla lobes or magenta with a white throat; tubular-infundibuliform, 4.6–9.5 cm long and 0.9–2.4 cm wide at the mouth, the tube 3.1–6.8 cm long, the lobes 1.3–3.2 cm long; lepidote inside and out, glandular-pubescent at and below the level of stamen insertion inside, stamens didynamous, the anther thecae divaricate, each 3.5–4.5 mm long, the longer filaments 1.8–2.1 cm long, shorter filaments 1.0–1.3

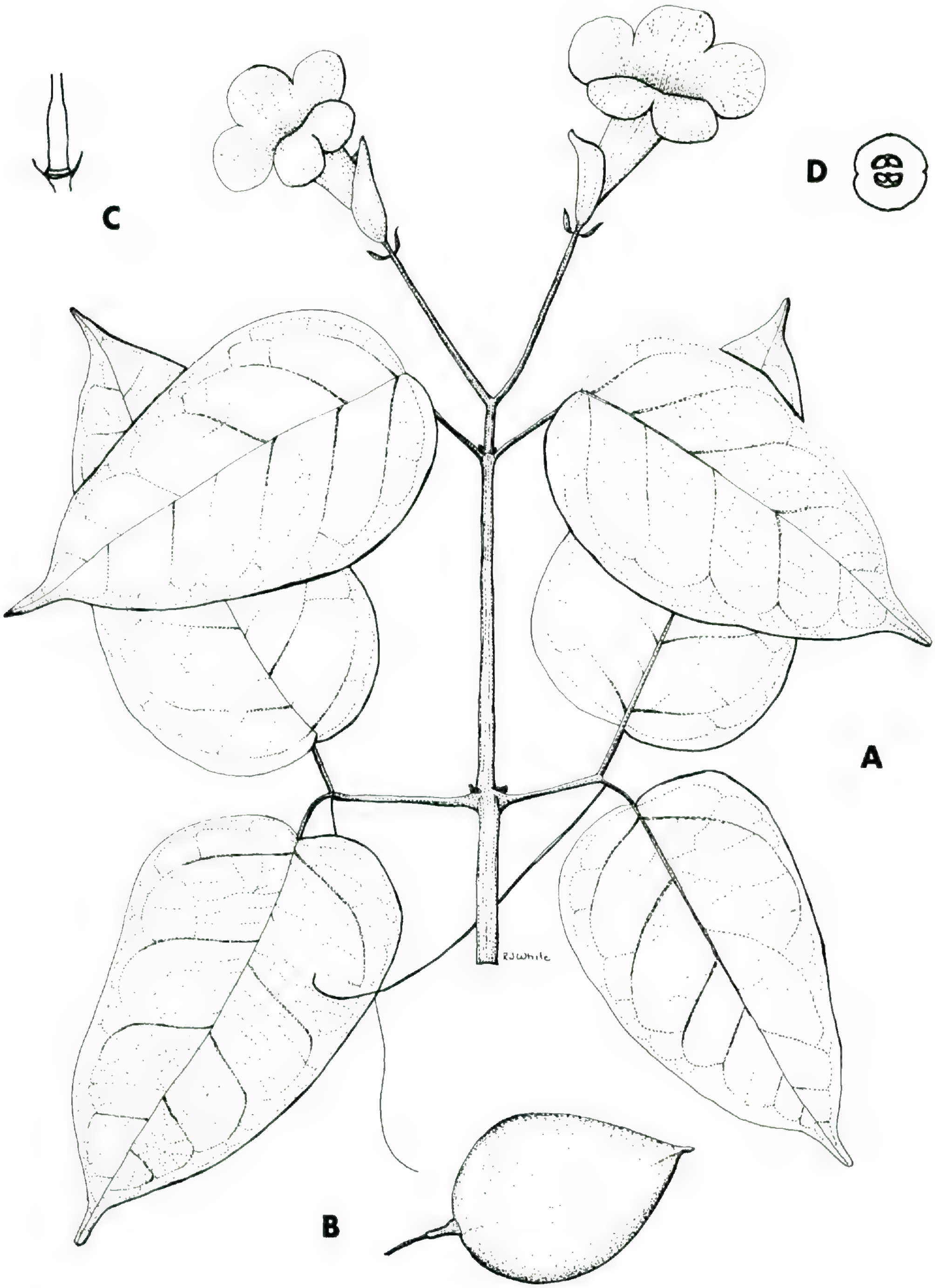


FIGURE 26. *Phryganocydia*.—A–B. *P. phellosperma* (Hemsl.) Sandw.—A. Habit (× ½). [After *Stern et al. 59* (MO).]—B. Fruit (× ½). [After *Dwyer 1093* (MO).]—C–D. *P. corymbosa* (Vent.) Bur. *ex* K. Schum.—C. Ovary (× 2½).—D. Ovary cross section (× 9). [After *Gentry 1450* (MO).]

cm long, the staminode 2–3 mm long, inserted 0.8–1.2 mm from base of corolla tube, pistil 3.8–4.1 cm long, ovary linear, 3–4 mm long and 1 mm wide, lepidote, the ovules 2-seriate in each locule; disc obsolete. *Capsule* linear-oblong, acute, flattened, 13–53 cm long and 1.4–2.3 cm wide, densely lepidote, appearing grayish, crystalline-rough under a lens, neither margins nor midrib pronounced; seeds 1.5–2.0 cm long and 4.7–7.3 cm wide, the wings membranaceous but brown, not demarcated from the seed body.

The distribution of this species is enigmatic. It is the commonest species of Bignoniaceae in the Canal Zone and much of eastern Panama and is abundant through the tropical moist forest of eastern Panama, occurring also to some extent in tropical wet forest. However, it has never been collected west of Coclé Province and is apparently absent from Costa Rica. It is thus the only species of Bignoniaceae of the tropical moist forest life zone which occurs in Panama but not Costa Rica; this is doubly surprising considering its extreme abundance. To the south its range extends to Brazil. The species flowers throughout the year. Fruit maturation takes about two months, and seed release occurs, like flowering, throughout the year.

The fruit of this species is similar to that of *Cydista aequinoctialis*, but the valves tend to be gray rather than black as in *C. aequinoctialis;* they also curl upon falling while the valves of the latter merely bend up at the sides. Under a lens the fruits of this species have an irregular, almost crystalline surface texture, while those of *C. aequinoctialis* are smooth-textured. The seeds are also distinguishable, but with difficulty—in this species they have a submarginal hilum with the seed body relatively far from it, while seeds of *C. aequinoctialis* have a nearly marginal hilum with the body of the seed crowded against it. In sterile condition *P. corymbosa* can be distinguished best by its tendency to flattened, almost alate, petiolules and terete, smooth, light gray twigs. The leaves have a characteristic shape and waxy appearance that becomes readily recognizable after sufficient exposure.

CANAL ZONE: Barro Colorado Island, *Aviles 83* (F), *90* (MO), *990* (F); *Bailey & Bailey 314* (F), *608* (F, GH); *Bangham 387* (A, F, US); *Brown 20* (F); *Croat 4975* (MO, SCZ), *5405* (MO), *5459*, *5542*, *5590*, *6089*, *6591* (all MO, SCZ), *7119* (MO), *7267* (MO, SCZ), *7870*, *7988*, *8168*, *8272*, *8437*, *12684*, *13228* (all MO); *Foster 964* (PMA); *Frost 94* (F); *Gentry 431* (MO, WIS), *711*, *1989* (both MO); *Hayden 19* (MO); *Kenoyer 526* (US); *Salvoa 849* (A); *Shattuck 466*, *515*, *784*, pro parte (all F, MO), *990* (MO, US), *1042* (F, MO); *Standley 51126* (A, US); *Starry 210* (F, MO); *Wetmore & Woodworth 32*, *73* (both F), *853*, *876*, *878*, *909* (all A); *Woodson & Schery 976* (MO); *Woodworth & Vestal s.n.* (F), *376* (A, F), *394* (A, MO), *577* (A). Near Fort Kobbe, *Allen 2020* (GH, MO). Río Chilibre between Juan Mina and Madden Dam, *Bartlett & Lasser 16414* (MO). Vicinity of Albrook tower, *Blum 436* (MO, SCZ); *Cowell 206* (NY). Gatún, *Cowell 313* (NY, US). Road S-11 NW of Escobal, *Croat 12459* (MO, SCZ). Fort Sherman hill C-6, *Duke 4403* (GH, K, MO). Ancon Hill, *Duke 4580* (GH, K, MO). Albrook site, *Dwyer 7114* (GH, MO, US). Las Cruces trail in Madden Forest, *Gentry 1382* (MO). Pipeline road, *Gentry 1416*, *1584* (both MO). Boy Scout road near Madden Lake, *Gentry 2056* (MO). Between Summit and Gamboa, *Greenman & Greenman 5262* (MO). Paraíso Station, Panama Railroad, *Hayes 158* (GH), *222* (BM, K). Summit, *Hayes 591* (NY). Ancon Hill, *Killip 3055* (F, US). Pipeline road, *Lewis & Sharp 32* (MO). Near Fort Randolph, *Maxon & Harvey 6502* (US). Around Culebra, *Pittier 2150* (US). Cerro Gordo near Culebra, *Standley 25952* (MO, US). Summit, *Standley 26959* (US). Corozal, *Standley 27350* (US). Las Cascades Plantation near Summit, *Standley 29680* (US). East Paraíso, *Standley 29836* (US). Vicinity of Summit, *Standley 30093* (A,

US), *30104* (US). Albrook Air Force Base, *Tyson s.n.* (SCZ), *1412* (MO, SCZ). Pipeline road, *Tyson 1482* (MO, SCZ). Fort Sherman along road S-5, *Tyson & Dwyer 1226* (MO). Along road between Cocoli and Contractor's Hill, *Tyson & Dwyer 6489* (SCZ). Without locality, *Johansen 40* (GH, US). COCLÉ: Bismarck above Penonomé, *Williams 550* (US). COLÓN: Santa Rita Ridge, *Gentry 1863, 1885* (both MO). E of Río Piedras on road to Portobelo, *Gentry 2189* (MO). Between Río Piedras and Puerto Pilón, *Lewis et al. 3213* (MO, SCZ); *Nee & Mori 3668* (MO). DARIÉN: Trail between Pinogana and Yavisa, *Allen 279* (MO). Vicinity of Boca de Cupe, *Allen 888* (F, GH, MO, NY, US). Vicinity of Santa Fé on Río Sabana, *Duke 4112* (MO). Between Ríos Membrillo and Subcutí, *Duke 8588* (MO). Río Balsa between Río Aretí and Manene, *Duke 8781* (MO). Vicinity of Piñas, *Duke 10635* (MO). Río Balsa between Manene and Tusijuanda, *Duke 13565, 13568* (both MO). Río Mortí, *Duke 14179* (F, MO, NY). Camp Lagarto, *Duke 15201* (MO). Around La Palma, *Gentry 3923* (MO). Isla Lagarto in Golfo de San Miguel, *Gentry 3998* (MO). Second large point just before Punta Alegre NE of Garachiné, *Gentry 4062* (MO). S of Jaqué, *Gentry 4104* (MO). Ridge from top of Cerro Pavarandó to top of Cerro Derumba, *Gentry 4205, 4215* (both MO). S of La Palma, *Gentry 4304* (MO). Río Paya from Río Tuira to village of Paya, *Gentry 4380* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4400* (MO). Below Boca de Cupe on Río Tuira, *Gentry 4488* (MO). Below Boca de Yape on Río Tuira, *Gentry 4489* (MO). Midway between Yavisa and El Real on Río Chucunaque, *Gentry 4506* (MO). El Real, *Gentry 4524, 4578* (both MO). Near Cerro Pirre on Río Parasenico, *Gentry 4687* (MO). Vicinity of La Palma, *Pittier 6693, 6978* (both US). PANAMÁ: Río Maestra, *Allen 48* (A, MO). Vicinity of Bejuco, *Allen 976* (MO, US). Vicinity of Campana, *Allen 3571* (BR, C, GH, K, MO, NY, P, U, US). Cerro Campana, *Correa & Dressler 391* (PMA). Between Capira and Chorrera, *Dodge 10714* (F, MO). Along road between Panamá and Chepo, *Dodge 10730* (MO). Along banks of Quebrada La Palma and cañon of Río Chagres, *Dodge & Allen 17346* (MO). Río Cañita, *Duke 3812* (MO, SCZ). E of Chepo, *Duke 4046* (MO), *4079* (K, MO). Río Pita above confluence with Río Maestra, *Duke 4737* (MO). Along Río Terable and road to El Llano, *Duke 5660* (GH, MO). San José Island, *Duke 12555* (MO); *Erlanson 7* (BM, NY, US); *Harlow 4* (US), *30* (GH, US); *Johnston 164* (BM, GH, MO, US), *317* (BM, MO, US), *1263* (GH); *Tyson & Loftin 5063* (SCZ). Near Cañitas, *Gentry 1406, 4966* (both MO). Río Pasiga, *Gentry 2202, 2259, 2299* (all MO). Río Maestra, *Gentry 2211* (MO). E of Chilibre, *Gentry 2508* (MO). Río Piragua (Tabardí), *Gentry 2529* (MO). Icantí, *Gentry 2616* (MO). 10–15 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3833* (MO). W of Chepo, *Gentry & Tyson 1639* (MO). Dam site on Río Bayano, *Gentry & Tyson 1665* (MO). Punta Paitilla, *Heriberto 211, 228* (both US). Chimán, *Lewis et al. 3342* (MO, SCZ). Trapeche Island, *Miller* 1887 (US). Near Chepo, *Pittier 4653* (BM, C, GH, NY, US). Near road to Cerro Azul, *Rivas 10* (MO, PMA). Las Cumbres, *Rivera 13* (GH, MO, PMA). Villa Rosario, *Saldana 31* (PMA). Vicinity of Arenoso on lower Río Trinidad, *Seibert 606* (A, K, MO, NY). Perlas Islands, without locality *Stevenson 409* (F). SAN BLAS: Isla Soskatupu, *Duke 8954* (MO). Ailigandí, *Dwyer 2831* (MO). Above Puerto Obaldía, *Gentry 1489* (MO). Mainland opposite Playón Chico, *Gentry 6416* (MO). Soskatupu, *Kirkbride 191* (MO, NY, SCZ). WITHOUT LOCALITY: *Duchassaing s.n.* (P).

2. **Phryganocydia phellosperma** (Hemsl.) Sandw., Kew. Bull. 1940: 302. 1941. —FIG. 26A–B.

Macfadyena phellosperma Hemsl., Biol. Centr. Amer. Bot. 2: 492. 1882. TYPE: Panama, Canal Zone, *Hayes 81* (BM, K).

Liana to 2.5 cm in diameter, the bark smooth, gray, longitudinally lightly striated; stem with 4 phloem arms in cross section; branchlets subterete or somewhat flattened, reddish-brown, lepidote, lacking conspicuous lenticels, interpetiolar glandular fields lacking; pseudostipules lacking. *Leaves* 2-foliolate, occasionally simple, sometimes with a tendril; leaflets ovate, long-acuminate, shallowly cordate to rounded, 5.1–13 cm long and 3.5–8 cm wide, coriaceous to subcoriaceous, secondary veins 4–6 on a side, lepidote above and beneath, otherwise glabrous, grayish olive when dry, midvein below reddish-brown, the lateral veins inconspicuous; tendril simple, 8–15 cm long; petiolules 0.8–2.2 cm

long, petiole 0.8–3.8 cm long, ± lepidote. *Inflorescence* 1–2 terminal flowers, the pedicels lepidote. *Flowers* fragrant, sweet-smelling, the calyx spathaceously split from near the tip to 2 mm from the base, the blunt tip bent slightly away from the corolla, inconspicuously lepidote, 1.8–2.8 cm long and 0.5–1.1 cm wide at widest point; corolla lavender with a white throat and magenta spot at the base of the upper corolla lobes, the throat with 9 very fine magenta nectar guides; tubular-infundibuliform, 4.2–7 cm long and 1.1–2.3 cm wide at the mouth of tube, the tube 3–4.7 cm long, the lobes 1.2–2.5 cm long; inconspicuously lepidote outside, the lobes pubescent on the margins and sparsely within, the tube mostly glabrous inside, glandular-pubescent at and below the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 1.3–1.5 cm long and inserted 0.4–0.5 cm from the base of the tube, the shorter filaments 0.8–1.1 cm long and inserted 0.2 cm from base of tube, the staminode to 4 mm long, inserted 1 mm from base of tube or absent; pistil 2.0–2.2 cm long, the ovary rounded-conical, 1.5 mm long and 1.5 mm wide, 1.5 mm thick, lepidote, the ovules 2-seriate; disc lacking. *Capsule* (including extralimital material) broadly ovoid to almost suborbicular, slightly compressed, 3.5–6.5 cm long and 3.7–5.6 cm wide, densely lepidote, crystalline-rough under a lens, drying yellowish; seeds thick, corky, wingless, with a loose epidermis which pulls away from the seed body, 2.0–2.7 cm long and 2.2–3.5 cm wide, the hilum large, to 8 mm by 15 mm.

Ecologically restricted to mangrove swamp habitats, *P. phellosperma* occurs only along the Pacific coast from Colombia to Costa Rica. It is locally abundant but rarely collected. It flowers mostly in the wet season from late May through July, although occasional flowers are produced throughout the year. The seeds are water-dispersed.

It is closely related to *P. corymbosa* and quite probably derived from it. The two similar congeners occasionally overlap ecologically at the edge of the mangrove consociation, but the much more coriaceous, long-acuminate leaflets of *P. phellosperma* serve to distinguish it. The flowers of the two species are nearly identical, although those of *P. phellosperma* are usually smaller and have a more blunt-tipped calyx. The fruits are much shorter and thicker than those of *P. corymbosa*. Thus *Phryganocydia* parallels *Tabebuia* and other genera with species specialized to live in mangrove consociations; these specializations are reflected in corky, more or less wingless seeds which are water-dispersed and short, thick fruits.

CANAL ZONE: Near Balboa, *Alston 8830* (BM, K). Ancón, *Bangham 609* (A). Miraflores locks, *Dwyer 1093* (MO). W end of Thatcher Ferry Bridge, *Gentry 745* (MO, SCZ). Farfan Beach road, *Gentry & Dwyer 3551* (MO). Río Grande swamp, *Hayes 81* (BM, K). Near Miraflores locks, *Stern et al. 59, 80* (both GH, K, MO, US). Río Grande, *Woodson et al. 761* (A, MO, NY). DARIÉN: Chepigana, *Duke 279* (MO). Along Río Tuira 5–15 mi. downstream from El Real, *Duke 4947* (BM, GH, MO, US). Punto Sabanas across bay from La Palma, *Gentry 3959, 4089A* (both MO). Isla Encanto in Golfo de San Miguel, *Gentry 4008* (MO). Río Sabanas below Santa Fé, *Gentry 4082* (MO). Punta Triunfo up Río Sabanas, *Gentry 4085* (MO). Mouth of Río Jaqué, *Gentry 4190* (MO). PANAMÁ: San José Island, Mouth of Río Marino, *Johnston 1296* (GH). Playa del Palma near San Carlos beach, *Lewis et al. 1502* (GH, MO, US). Taboga Island, *Pittier 3611* (GH, US).

27. PITHECOCTENIUM

Pithecoctenium Mart. *ex* Meisn., Gen. 1: 300; 2: 208. 1840. LECTOTYPE: *P. echinatum* (Jacq.) Baill.

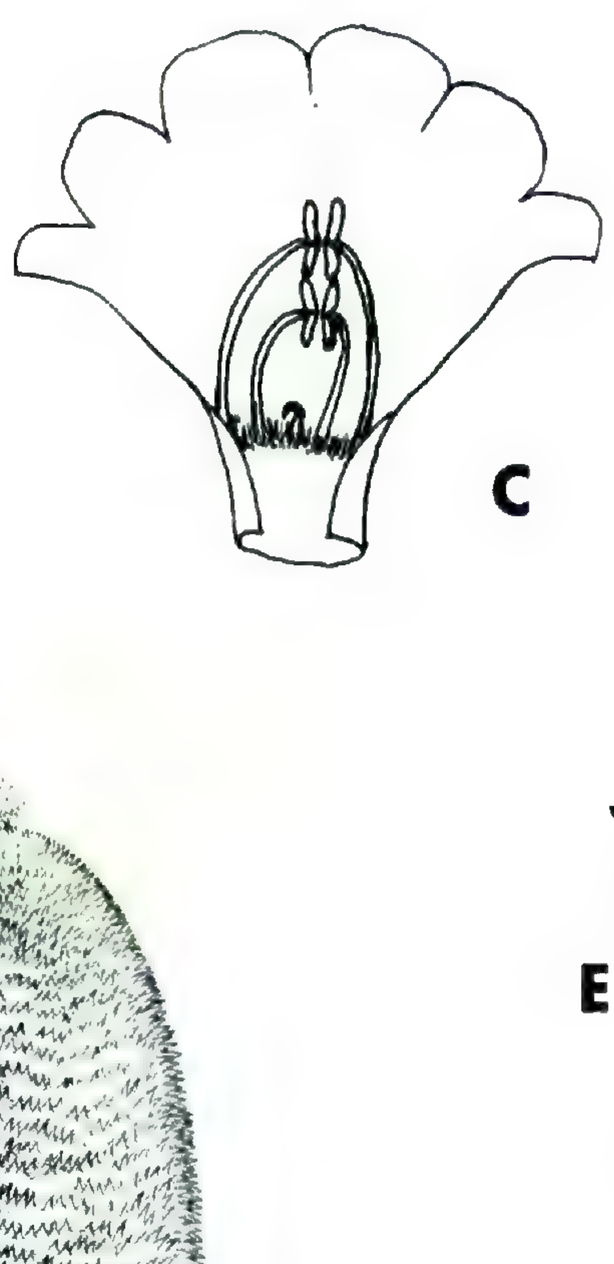
Liana; stem with 4 phloem arms in cross section; branchlets acutely hexagonal with detachable ribs, without interpetiolar glandular fields; pseudostipules spathulate, not persistent. *Leaves* 2–3-foliolate, the terminal leaflet often replaced by a trifid tendril, this often divided to at least 15-fid, some of the tendril-ends often with thickened discs which attach the vine to a support. *Inflorescence* a terminal raceme or racemose panicle. *Flowers* with the calyx cupular, truncate, thick, more or less minutely 5-denticulate, lepidote and puberulous; corolla white, relatively thick, tubular-campanulate, densely pubescent outside, anthers glabrous, the thecae straight, divaricate; pollen grains esulcate, the exine alveolate, ellipsoid-cylindric, contracted above the disc, densely appressed simple-pubescent, the ovules multiseriate in each locule; disc annular-pulvinate. *Fruit* a thick, woody, somewhat compressed, elliptic capsule, the valves parallel to the septum, densely echinate; seeds alate with a thin body surrounded by a broad clearly demarcated hyaline-membranaceous wing.

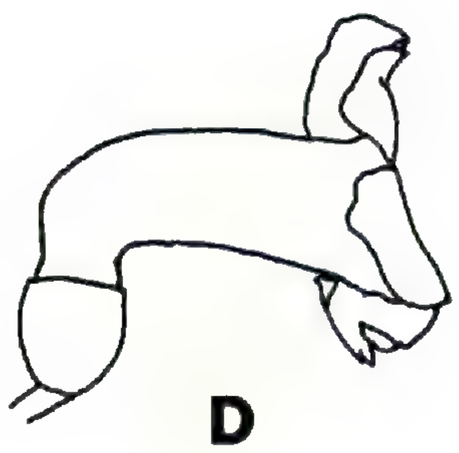
Three or four species in continental tropical America ranging from Mexico to Argentina and Brazil.

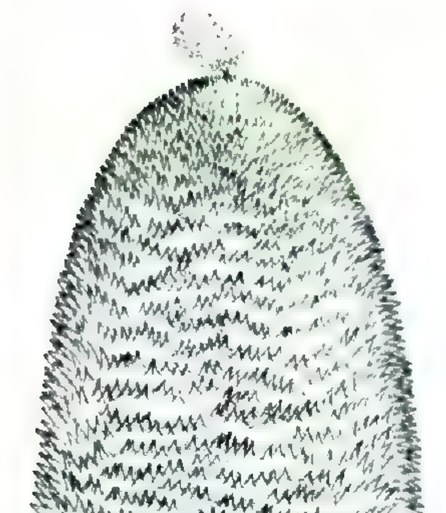
1. **Pithecoctenium echinatum** (Jacq.) Baill., Hist. Pl. 10: 8. 1888.—FIG. 27.

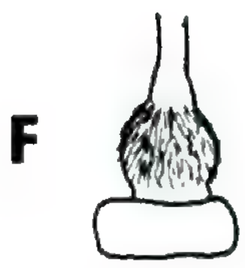
Bignonia echinata Jacq., Enum. Pl. Carib. 25. 1760; Sel. Stirp. Amer. 183, *tab. 176, fig. 52.* 1763. TYPE: Colombia, Cartagena (not seen).
B. tiliaefolia H.B.K., Nov. Gen. Sp. Pl. 3: 136. 1819. TYPE: Venezuela, Orinoco (?), *Humboldt & Bonpland* (P).
B. squalus Vell., Fl. Flum. 230. 1825; 6: *tab. 13.* 1827. TYPE: Brazil (not seen).
B. phaseoloides Cham., Linnaea 7: 698. 1832, fide Bur. & K. Schum. TYPE: Brazil, *Sellow s.n.* (not seen).
B. hexagona DC., Rev. Bign. (Bibl. Univer. Genève) 21. 1838, nomen nudum.
B. muricata Moc. *ex* DC., Rev. Bign. (Bibl. Univ. Genève) 22. 1838, nomen nudum.
Pithecoctenium aubletii Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 12. 1842. TYPE: Based on *Bignonia echinata* Aubl., the fruit of which is *P. echinatum* but the leaves and flowers *Arrabidaea inaequalis* (DC. *ex* Splitg.) K. Schum.
P. phaseoloides (Cham.) Schenk *in* Schimper, Bot. Mittheil. 4: 193. 1842.
P. cordifolium Mart., Flora 24(2): Beibl. 48. 1841. TYPE: Brazil, Cujaba, *Martius 516* (MO, NY).
P. hexagonum DC., Prodr. 9: 195. 1845. TYPE: Mexico, Chalco, *Andrieux 222* (G-DC, K).
P. lundii DC., Prodr. 9: 196. 1845. TYPE: Brazil, São Paulo, *Lund 876* (G-DC).
P. muricatum Moc. *ex* DC., Prodr. 9: 194. 1845. TYPE: Mexico (not seen).
P. squalus (Vell.) DC., Prodr. 9: 194. 1845.
P. tribrachiatum Loes., Fedde Repert. 16: 209. 1919. SYNTYPES: Mexico, Veracruz, *Schenck 860, 861* (not seen).
P. glaucum Rusby, Mem. New York Bot. Gard. 7: 354. 1927. TYPE: Bolivia, Rurrenabaque, *Cardenas 2063* (K, NY, US).

Liana to at least 10 cm in diameter, the bark loose, fibrous, vertically striate, becoming a spirally twisted bush rope; stem with 4 phloem arms in cross section; branchlets sharply hexagonal with the angles ribbed, lepidote with occasional simple trichomes, the nodes without interpetiolar glandular fields, some-









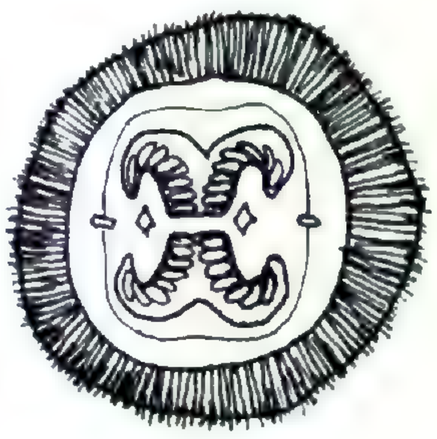


FIGURE 27. *Pithecoctenium echinatum* (Jacq.) K. Schum.—A. Habit (× 2/5). [After *Croat 5804* (MO).]—B. Fruit (× 2/5). [After *Croat 7022* (MO).]—C. Corolla split open (× 3/5).—D. Fresh corolla in side view (× 3/5).—E. Pistil (× 3/5).—F. Ovary and disc (× 1 1/5).—G. Ovary cross section (× 6 3/5). [After *Gentry 2701* (MO).]

times with a ridge connecting opposite petioles; pseudostipules elongate, ca. 10 mm long and 2 mm wide, caducous on mature twigs. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets ovate to subrotund, acuminate, cordate, 3.3–18 cm long and 2.0–14.7 cm wide, membranaceous, palmately veined at the base, the secondary veins 4–6 on a side, strongly lepidote above and beneath, variably pubescent above and beneath with simple trichomes usually at the base of main nerves and sometimes scattered over the surface, plate-shaped glands in the axils of basal nerves beneath, more or less olive when dry; tendril trifid to 15-fid (perhaps more), 4–12 cm long to first branching, the ultimate tips often thickened into discs which attach to bark of supporting tree; petiolules and petiole tetragonal, the former 1.6–7.0 cm long, the latter 2.9–7.2 cm long, lepidote and usually simple-pubescent at least on the angles. *Inflorescence* a few- to 15-flowered terminal raceme or racemose panicle with small, caducous bracts, the rachis and pedicels lepidote and simple-pubescent. *Flowers* with musky odor, calyx cupular, coriaceous, truncate to inconspicuously 5-denticulate with submarginal teeth, lepidote and densely pubescent, 8–12 mm long and 9–11 mm wide, eglandular; corolla white with yellow throat, relatively thick and fleshy, especially the basal 0.9–1.2 cm, tubular-campanulate but usually bent at 90° angle in the middle, 3.6–6.1 cm long and 1.0–1.8 cm wide at the mouth, the tube 1.2–1.7 cm to the bend, 2.2–3.5 cm long above the bend, the lobes 0.6–1.7 cm long, densely pubescent with more or less moniliform trichomes outside, inside moniliform-pubescent on the lobes, the tube glabrous except for dense moniliform trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 1.7–2.1 cm long, shorter filaments 1.2–1.7 cm long, the staminode 0.6–0.8 mm long, inserted 0.8–1.2 mm from the base of the corolla tube; pistil 3.3–3.5 cm long, stigma heart-shaped, 4 mm by 4 mm, ovary short-cylindric, swollen at the middle, 5–6 mm long and 4 mm wide at the middle, 3 mm wide at the base and apex, densely simple-pubescent with multicellular trichomes, the ovules ± 15-seriate in each locule; disc annular-pulvinate, 2–3 mm long and 6 mm wide. *Capsule* rounded-oblong to elliptic, 12–31 cm long and 5.2–7.5 cm wide, to 3.5 cm thick, the surface strongly echinate-tuberculate, sometimes with a few simple trichomes at the base of tubercles; seeds 2.3–4.1 cm long and 4.5–9.5 cm wide, the wings surrounding the seed body, membranaceous, hyaline except the extreme base, clearly demarcated.

Both geographically and ecologically this is one of the most wide-ranging species of Bignoniaceae, although never extremely abundant. It occurs from Mexico to Argentina. It flowers during the wet season, mostly in May and June but was collected in full bloom in several places at Almirante, Bocas del Toro, in late November. The fruits take almost a year to mature, and seeds are released in mid dry season from February through April. Robin Foster (personal communication) considers *P. echinatum* to be the most effectively wind-dispersed species occurring on Barro Colorado Island. The lightness and aerodynamic stability of a floating seed of this species make its path of descent a thing of beauty even in perfectly still air; with a breeze a seed remains air-

borne indefinitely. The dispersability of its seeds must be in large part responsible for the great geographic distribution of the species.

This species is distinguished from all other Central American species except *Amphilophium* by its sharply hexagonal twigs. Its elongate pseudostipules, usually much-branched tendrils and lack of dendroid trichomes serve to differentiate it from the two species of *Amphilophium*. The bent white corolla and large echinate fruits are distinctive. "Peine de mono," "monkey's hairbrush."

BOCAS DEL TORO: Vicinity of Almirante, *Gentry 2701, 2752, 2783* (all MO). CANAL ZONE: Barro Colorado Island, *Croat 5804* (MO, NY, SCZ), *5837* (MO), *7022* (MO, SCZ), *9418* (MO, SCZ), *10851, 14066* (both MO), *15115* (MO); *Foster 840* (MO, PMA), *1173* (MO, PMA); *Wetmore & Woodworth 36* (A, F). Las Cruces Trail in Madden Forest, *Gentry 1381* (MO). Road K-19, *Gentry 1791* (MO). Boy Scout road near Madden Lake, *Gentry 2059, 2060* (both MO). Fort Sherman, *Gentry & Tyson 4841* (MO). CHIRIQUÍ: Finca Boquete, *Oppenheimer & Hladik 209* (MO). COLÓN: Ridge W of Portobelo, *Gentry 1762* (MO). DARIÉN: Near Jaqué, *Gentry 4177* (MO). Slopes of Cerro Chucula, drainage of Río Pavarandó, *Gentry 4263* (MO). Below Paya on Río Paya, *Gentry 4392* (MO). El Real, *Gentry 4504* (MO). PANAMÁ: Río Maestra, *Gentry 2221, 2230A* (both MO). Río Pasiga, *Gentry 2252, 2270* (both MO). Río Piragua (Tabardí), *Gentry 2532* (MO). Icantí, *Gentry 2597* (MO). Near Río Espavé, *Gentry 3789* (MO). Farfan Beach road, *Gentry & Dwyer 3556* (MO). SAN BLAS: Above Puerto Obaldía, *Gentry 1476, 1559* (both MO). VERAGUAS: Above Santa Fé on slopes of Cerro Tuté, *Gentry 6256* (MO).

28. PLEONOTOMA

Pleonotoma Miers, Proc. Roy. Hort. Soc. 3: 184. 1863. LECTOTYPE: *P. jasminifolia* (H.B.K.) Miers.

Lianas; stems with 4 phloem arms in cross section, the extreme center hollow; branchlets acutely tetragonal with detachable ribs, without interpetiolar glandular fields; pseudostipules foliaceous or absent. *Leaves* biternate or triternate or ternately bipinnate or tripinnate, the terminal pinna often replaced by a trifid tendril. *Inflorescence* an axillary or terminal raceme. *Flowers* with the calyx cupular, truncate, usually minutely denticulate; corolla white to pale yellow, narrowly campanulate-infundibuliform, the tube glabrous or variously pubescent in upper part; anthers glabrous, the thecae straight, divaricate; pollen grains 3-colpate, the exine microreticulate; ovary oblong, more or less lepidote or pubescent, the ovules 2-seriate in each locule; disc cupular-pulvinate. *Fruit* an elongate-linear to elongate-oblong compressed capsule, the valves parallel to the septum, more or less smooth, drying blackish, the median nerve inconspicuous; seeds thin, bialate, the wings membranaceous, brown, poorly demarcated from the seed body.

Ten to twelve species in continental tropical America ranging from Costa Rica to Argentina.

1. **Pleonotoma variabilis** (Jacq.) Miers, Proc. Roy. Hort. Soc. 3: 184. 1963. —FIG. 28.

Bignonia variabilis Jacq., Hort. Schoenb. 2: 45, *tab. 212*. 1797. TYPE: Venezuela, Caracas, *Jacquin s.n.* (W).

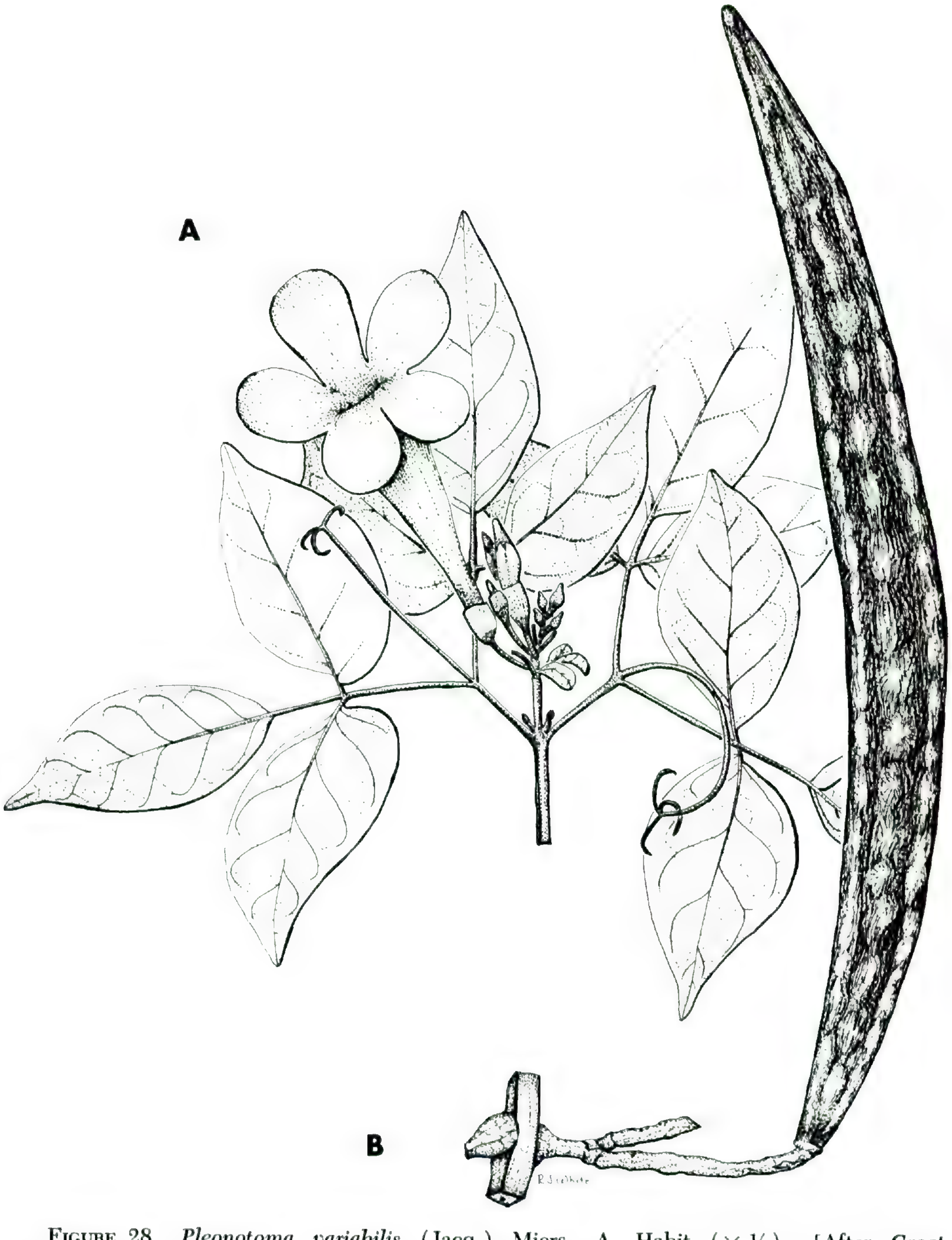


FIGURE 28. *Pleonotoma variabilis* (Jacq.) Miers.—A. Habit (× ½). [After *Croat 5607* (MO).]—B. Fruit (× ½). [After *Gentry 3972* (MO).]

Liana to at least 3 cm in diameter, bark fibrous; stem with 4 phloem arms in cross section, extreme center hollow; branchlets acutely tetragonal with the angles ribbed, brown to green with ribs usually blackish, the nodes without interpetiolar glandular fields, a linear ridge connecting opposite petioles; pesudostipules narrow, 3–5 mm long and 1 mm wide, often deciduous. *Leaves* 3-

ternate or 2-ternate with a tendril or tendril scar; leaflets elliptic to elliptic-ovate, acute to acuminate, widely cuneate to asymmetrically truncate, 2.1–16 cm long and 0.8–9.5 cm wide, secondary veins 5–7 on a side, with scattered lepidote scales, slightly puberulous along the veins above, beneath usually with simple trichomes in the axils of lateral nerves and sometimes along the main veins, greenish when dry; tendril trifid, 2–14 cm long to branching, the 3 arms 0.1–2.1 cm long; petiole, petiolules, and subpetiolules all strongly angled, lepidote to puberulous, the terminal subpetiolule 0.3–4.8 cm long, laterals 0.2–2.2 cm long, the terminal petiolule 2.5–6.5 cm long, lateral 1.2–6.5 cm long, the petiole 2.1–6.7 cm long. *Inflorescence* a short, long-pedicelled raceme, usually terminal, the pedicels and peduncle mostly glabrous, somewhat simple-pubescent at the nodes. *Flowers* with the calyx cupular, more or less truncate, 5–9 mm long and 5–8 mm wide, mostly glabrous, more or less ciliate, sometimes with scattered lepidote scales and with glands in the upper third; corolla white or cream with light yellow tube, tubular-infundibuliform, 6.4–10.2 cm long and 1.3–2.7 cm wide at the mouth, the tube 4.5–7.0 cm long, the lobes 1.4–2.2 cm long, tube glabrous outside, the lobes glandular-lepidote and puberulous with plate-shaped glands outside at the base, tube glabrous within except for long simple multicelled trichomes at and below the level of stamen insertion, in bud long-pointed, conspicuously pubescent at the tip; stamens didynamous, the anther thecae divaricate, ca. 5 mm long, the longer filaments 2.6–2.8 cm long, shorter filaments 1.7–1.9 cm long, the staminode 4–5 mm long, inserted 1.9–2.1 cm from the base of the corolla tube; pistil 4.3–5.5 cm long, the ovary linear-oblong, 4 mm long and 1.5 mm wide, lepidote, the ovules 2-seriate in each locule; disc annular-pulvinate, 1.5–2 mm long and 3–4 mm wide. *Capsule* linear to linear-oblong, acute, somewhat compressed, 15–30 cm long and 1.7–2.7 cm wide, 3–7 mm thick, lepidote, slightly and irregularly warty-tuberculate with shallow projections, drying dark; seeds 1.1–1.5 cm long and 3.0–5.0 cm wide, the wings membranaceous, brown, poorly demarcated from the seed body.

A vine of the tropical moist forest, premontane wet forest, and tropical wet forest, *P. variabilis* ranges from Costa Rica to Venezuela and Trinidad. It flowers during the dry season from February to May. Seed release is during the dry season, and young plants are relatively common.

This is the only vine in the family in Central America to have bicompound leaves. The leaves and strongly tetragonal stem make *P. variabilis* unmistakable, even in vegetative condition.

BOCAS DEL TORO: Along railroad between Almirante and Changuinola, *Gentry 2817* (MO). CANAL ZONE: Barro Colorado Island, *Croat 4006A, 5234, 5588, 6660, 7876, 7996A, 8133, 8247, 9147, 11083* (all MO); *Gentry 432* (MO). Pipeline road, *Gentry 1436* (MO), *Gentry & Dressler 1977* (MO). Fort Sherman, *Gentry & Tyson 4840, 4849* (both MO). DARIÉN: Vicinity of La Palma, *Gentry 3908, 4288* (both MO). Isla Lagarto in Golfo de San Miguel, *Gentry 3972* (MO). Isla Boca Grande in Golfo de San Miguel, *Gentry 4032* (MO). S of Jaqué, *Gentry 4097* (MO). Ridge from top of Cerro Pavarandó to Cerro Venado and Cerro Derumba, *Gentry 4213* (MO). Below mouth of Río Pucuro on Río Tuira, *Gentry 4326* (MO). Between Ríos Cube and Punusa, *Gentry 4458* (MO). El Real, *Gentry 4498, 4536* (both MO). Near Cerro Pirre on Río Parasenico, *Gentry 4758* (MO). Cana and vicinity, *Williams 796* (NY). LOS SANTOS: S of Macaracas, *Lewis et al. 1615* (MO). PANAMÁ: Finca Indio on slopes of Cerro Jefe, *Gentry 2152* (MO). Río Pasiga, *Gentry 2197, 2257, 2272* (all MO).

Río Maestra, *Gentry 2213, 2237* (both MO). Río Piragua (Tabardí), *Gentry* 2535 (MO). Río Bayano upriver from Río Piragua, *Gentry 2590* (MO). Icantí, *Gentry 2607* (MO). E of Cañitas, *Gentry 3695* (MO). Near Río Espavé, *Gentry 3708* (MO). Ca. 16 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3812* (MO). San José Island, *Johnston 1346* (GH, MO), *1400, 1412* (both GH). Along road between Empire and Chorrera, *Killip 3403* (US). SAN BLAS: Above Puerto Obaldía, *Gentry 1475, 1527* (both MO).

29. PODRANEA

Podranea Sprague *in* Thiselton-Dyer, Fl. Cap. 4(2): 449. 1904. TYPE: *P. ricolasiana* (Tanfani) Sprague.

Vines or climbing shrubs; branchlets terete without interpetiolar glandular fields; pseudostipules lacking. *Leaves* imparipinnately compound, without tendrils. *Inflorescence* a terminal panicle. *Flowers* with the calyx large, campanulate, membranaceous, strongly 5-toothed, pale lavender when fresh; corolla lavender with magenta markings, tubular-campanulate, glabrous outside; anthers glabrous, the thecae straight, divaricate; ovary linear, tetragonal, glabrous, the ovules ca. 6-seriate in each locule. *Fruit* a linear, leathery capsule dehiscing perpendicular to the septum.

One or two species of east tropical and southern Africa.

1. **Podranea ricolasiana** (Tanfani) Sprague *in* Thiselton-Dyer, Fl. Cap. 4(2): 450. 1904.—FIG. 29.

Tecoma ricolasiana Tanfani, Bull. Soc. Tosc. Ortic. 1887: 17. 1887. TYPE: (not seen).
Pandorea ricolasiana (Tanfani) Baill., Hist. Pl. 10: 40. 1888.

Vine or subscandent shrub. *Leaves* imparipinnately compound, usually 7–9 foliolate, without tendrils, the leaflets more or less ovate, obtuse to short-acuminate, serrate, truncate to cuneate or somewhat attenuate, 2.5–3.8 cm long and 1.5–2.0 cm wide, petiolulate. *Inflorescence* a terminal panicle. *Flowers* with the calyx large, cupular-campanulate, 1.5–2 cm long, strongly 5-dentate with apiculate lobes, pale lavender when fresh; corolla pale lavender or pinkish with a magenta patch at the base of the 2 adaxial lobes, the tube white with deep magenta lines inside and some pinkish splotches near the base, campanulate above a short cylindric base, 6–8 cm long, with scattered lepidote scales on the lobes, glandular-pubescent at the level of stamen insertion inside and pubescent with kinky trichomes in the sinuses between lobes, otherwise glabrous; stamens didynamous, the thecae divaricate, 3 mm long, the longer filaments 1.9–2.0 cm long, shorter filaments 1.4–1.5 cm long, the staminode 3 mm long, inserted ca. 10 mm from base of corolla tube; pistil 3.2–3.4 cm long, the ovary linear, glabrous, 5 mm long and 1.5 mm wide, the ovules 6-seriate in each locule; disc pulvinate, 0.5 mm long and 1.5–2.0 mm wide. *Capsule* (Sprague) linear and leathery.

This species is native to South Africa but is widely cultivated in tropical regions. It is a conspicuous ornamental, flowering through most of the year but seldom setting fruit in cultivation.

CHIRIQUÍ: Bambito, 1 mi. SW of Cerro Punta, *Tyson 5673* (MO, SCZ).

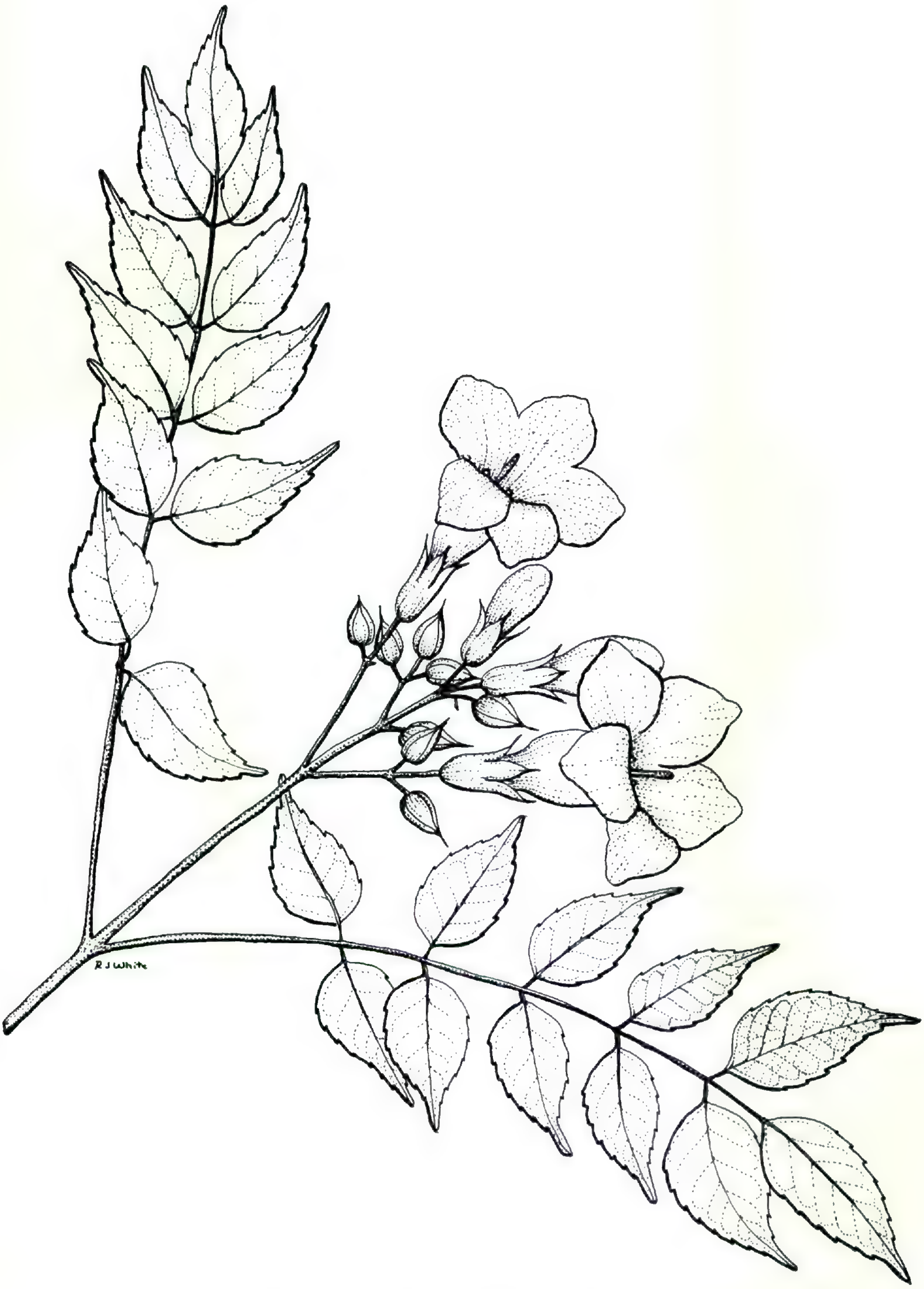


FIGURE 29. *Podranea ricolasiana* (Tanfani) Sprague, habit ($\times$ 7/10). [After *Gentry 473*, Costa Rica (MO).]

30. PYROSTEGIA

Pyrostegia K. B. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5. 3: 523. 1845. TYPE: *P. ignea* (Vell.) Presl = *P. venusta* (Ker.) Miers.

Lianas; branchlets subangulate with 6–8 inconspicuous ribs, without interpetiolar glandular fields, pseudostipules small and inconspicuous. *Leaves* 2-foliolate, often with a trifid tendril. *Inflorescence* a terminal or axillary panicle. *Flowers* with the calyx cupular, truncate, 5-denticulate, more or less glandular-lepidote; corolla orange-red, narrowly tubular-infundibuliform; stamens exserted, the anthers glabrous; pollen grains single, 4-colpate, the exine reticulate; ovary linear-tetragonal, lepidote; disc annular-pulvinate. *Fruit* compressed, linear, the valves parallel to the septum, smooth, the median nerve somewhat raised; seeds thin, bialate, the wings brown with hyaline margins.

Three or four species of tropical South America ranging from Brazil and Paraguay to southern Colombia.

1. **Pyrostegia venusta** (Ker.) Miers, Proc. Roy. Hort. Soc. 3: 188. 1863.—FIG. 30.

Bignonia venusta Ker., Bot. Reg. 3: 5. 249. 1818. TYPE: (not seen).
B. ignea Vell., Fl. Flum. 244. 1825; 6: *Tab. 15.* 1827. TYPE: (not seen).
Pyrostegia ignea (Vell.) K. B. Presl, Bot. Bemerk. 93. 1843.
P. acuminata Miers, Proc. Roy. Hort. Soc. 3: 188. 1863, nomen nudum.
P. intaminata Miers, Proc. Roy. Hort. Soc. 3: 188. 1863, nomen nudum.
P. pallida Miers, Proc. Roy. Hort. Soc. 3: 188. 1863, nomen nudum.
P. parvifolia Miers, Proc. Roy. Hort. Soc. 3: 188. 1863, nomen nudum.
P. reticulata Miers, Proc. Roy. Hort. Soc. 3: 188. 1863, nomen nudum.
Bignonia tecomaeflora Rusby, Mem. Torrey Bot. Club 6: 101. 1896. SYNTYPES: Bolivia, *Bang 1596* (K, GH, M, MO), *Bang 1510* (GH, MO, NY, US).

Liana; branchlets somewhat angled, puberulous, without interpetiolar glandular fields; pseudostipules inconspicuous or oblanceolate and subfoliaceous. *Leaves* 2-foliolate, sometimes with a terminal tendril; leaflets ovate, acute, basally rounded, 4–6 cm long and 2.5–4 cm wide, chartaceous, lepidote to more or less puberulous; tendril shortly trifid; petiolules 1–1.5 cm long, petiole 1.5–2.5 cm long. *Inflorescence* a terminal panicle. *Flowers* with the calyx cupular, subtruncate to 5 denticulate, scattered lepidote, the margin densely ciliate; corolla red-orange, tubular, the lobes narrow, valvate in bud, 5.5–6.5 cm long and 0.9–1.1 cm wide at the mouth, the tube 4.0–5.0 cm long, the lobes 1.0–1.5 cm long, the tube glabrous outside, the lobes conspicuously puberulous on margins and to some extent within, the tube pubescent inside at and below the level of stamen insertion; stamens exserted, the anther thecae not or very slightly divergent, ca. 4 mm long, the filaments 3.5–4.0 cm long, the staminode 3–4 mm long and inserted ca. 3 cm from base of tube, the filaments inserted 2.2–2.4 cm from base of tube; pistil 4.8–5.1 cm long, the ovary linear, lepidote, 4 mm long and 1 mm wide, the ovules 2-seriate in each locule but staggered so apparently 1-seriate in most cross sections; disc cupular-pulvinate. *Capsule* linear, acute at both ends, 25–30 cm long and 1.4–1.6 cm wide, the midrib slightly raised; seeds thin, bialate, 1.2–1.4 cm long and 4–4.5 cm wide, the wings brown with a hyaline tip.

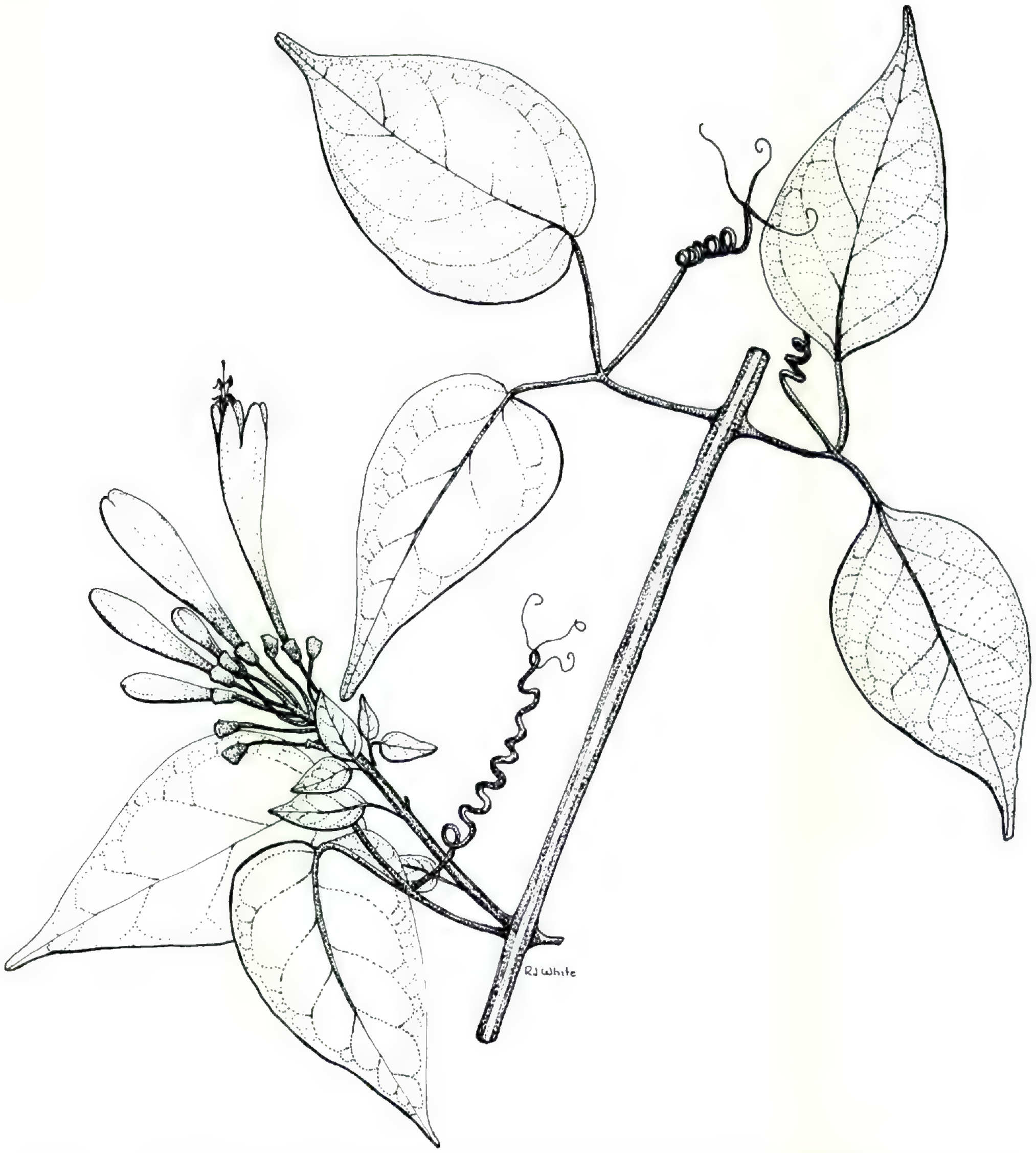


FIGURE 30. *Pyrostegia venusta* (Ker.) Miers, habit (× 3/5). [After *Gentry 472*, Costa Rica (MO).]

No collections have been seen from Panama, and the above description is taken from South American material. The species is widely cultivated in the neotropics, especially at middle elevations. I have seen it in Costa Rica, and it undoubtedly is cultivated in Chiriquí Province as well. It is native at least to Brazil, Paraguay, and Bolivia, but its natural range is obscured by extensive cultivation and sometimes naturalization. The conspicuous orange-red flowers with narrow corollas and exserted anthers are distinctive.

31. SARITAEA

Saritaea Dugand, Caldasia 3: 262. 1945. TYPE: *Arrabidaea magnifica* Sprague *ex* van Steenis or *Bignonia magnifica* W. Bull.

Lianas; branchlets terete without interpetiolar glands; pseudostipules conspicuous, foliaceous. *Leaves* 2-foliolate, often with a simple tendril. *Inflorescence* a few-flowered usually terminal corymbose panicle. *Flowers* with the calyx cupular, truncate, lepidote; corolla magenta, tubular-campanulate, glabrous or minutely glandular outside; anthers glabrous, the thecae straight, divaricate; ovary linear-cylindric, lepidote, the ovules 2-seriate in each locule; disc small, cupular-pulvinate. *Capsule* compressed, linear, the valves parallel to the septum; seeds thin, bialate, the wings hyaline-membranaceous.

One species of Colombia and Ecuador.

1. **Saritaea magnifica** (Sprague *ex* van Steenis) Dugand, Caldasia 3: 263. 1945.—FIG. 31.

Arrabidaea magnifica Sprague *ex* van Steenis, Recueil Trav. Bot. Néerl. 24: 830. 1927. TYPE: Colombia, Santa Marta, *Smith 741* (BM, K, US).

Liana; twigs subterete, flattened at nodes, lepidote, longitudinally finely striate, drying brown to gray, the nodes without interpetiolar glandular fields; pseudostipules foliaceous, conspicuous, 0.6–4.2 cm long and 0.4–2.0 cm wide. *Leaves* 2-foliolate, sometimes with a tendril or tendril scar; leaflets obovate, obtuse, narrowly cuneate to decurrent, 5.2–11.5 cm long and 3.1–6.4 cm wide, chartaceous, secondary veins 3–4 on a side, the lower pair almost straight and making a sharper angle with midvein, lepidote above and beneath with conspicuous glandular fields in the axils of the basal nerve pair beneath, drying olive green to olive brown above and beneath; tendril simple, 10–14 cm long; petiolules 0.3–1.6 cm long, petiole 1.7–2.8 cm long, lepidote as the petiolules. *Inflorescence* a few-flowered cymose panicle, terminal or axillary, its rachis and pedicels lepidote. *Flowers* sweetly aromatic; calyx cupular, truncate, 7–8 mm long and 6–7 mm wide, lepidote; corolla magenta, the throat white inside with magenta nectar guides, tubular-campanulate, 7.9–9.1 cm long and 1.6–2.0 cm wide at the mouth, the tube 5.6–6.3 cm long, the lobes 2.2–3.1 cm long, glabrous outside, pubescent inside at the level of stamen insertion with several-celled, apiculate trichomes; stamens didynamous, the anther thecae divaricate, 5.5–6 mm long, the longer filaments 2.7–2.9 cm long, shorter filaments 2.0–2.1 cm long, the staminode 4–6 mm long, inserted 9–12 mm from the base of the corolla tube; pistil 4.3–4.4 cm long, the ovary linear, 4 mm long and 1 mm wide, glandular-lepidote, the ovules 2-seriate in each locule but staggered so often appearing uniseriate in cross sections; disc cupular-pulvinate, 1 mm long and 2 mm wide. *Capsule* linear, compressed; seeds thin, bialate, the wings hyaline-membranaceous.

Native to Colombia but cultivated through much of the tropics, this species is a plant native to the New World which first became known to science as a cultivar in the Old World. For some time its origin remained a mystery, but it has since been found growing wild in Colombia and Ecuador.

The large, glabrous corolla, lack of interpetiolar glandular fields, and

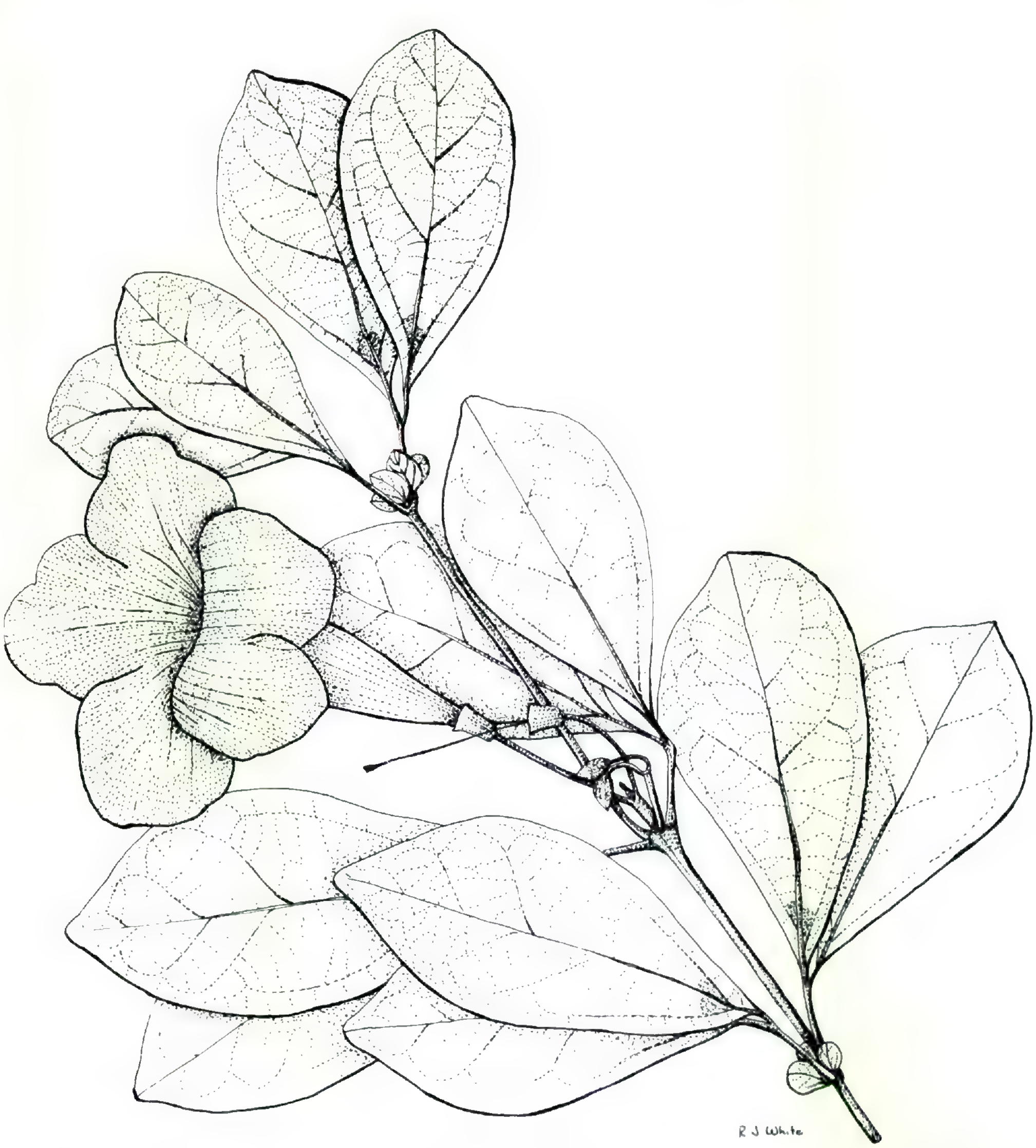


FIGURE 31. *Saritaea magnifica* (Spr. *ex* v. St.) Dugand, habit (× ⅔). [After *Gentry 6049* (MO).]

conspicuous pseudostipules indicate that its relationship may not be so much with *Arrabidaea*, near which it has been placed, as with *Cydista* and perhaps *Phryganocydia*. It has the simple tendrils and corolla form of *Cydista* and *Phryganocydia*, both of which tend to develop foliaceous pseudostipules. Its fruit is somewhat intermediate between that of *Arrabidaea* and that of *Cydista* and *Phryganocydia*. *Saritaea* has most of the characteristics one would expect of a predecessor to *Cydista* and, except for the calyx, to *Phryganocydia*. I suspect that it represents a link between these genera, which differ from it chiefly in lacking a nectiferous disc, and the complex of genera centered around *Arrabidaea*.

The cuneate, few-veined leaflets and conspicuous pseudostipules make the sterile plant easy to recognize.

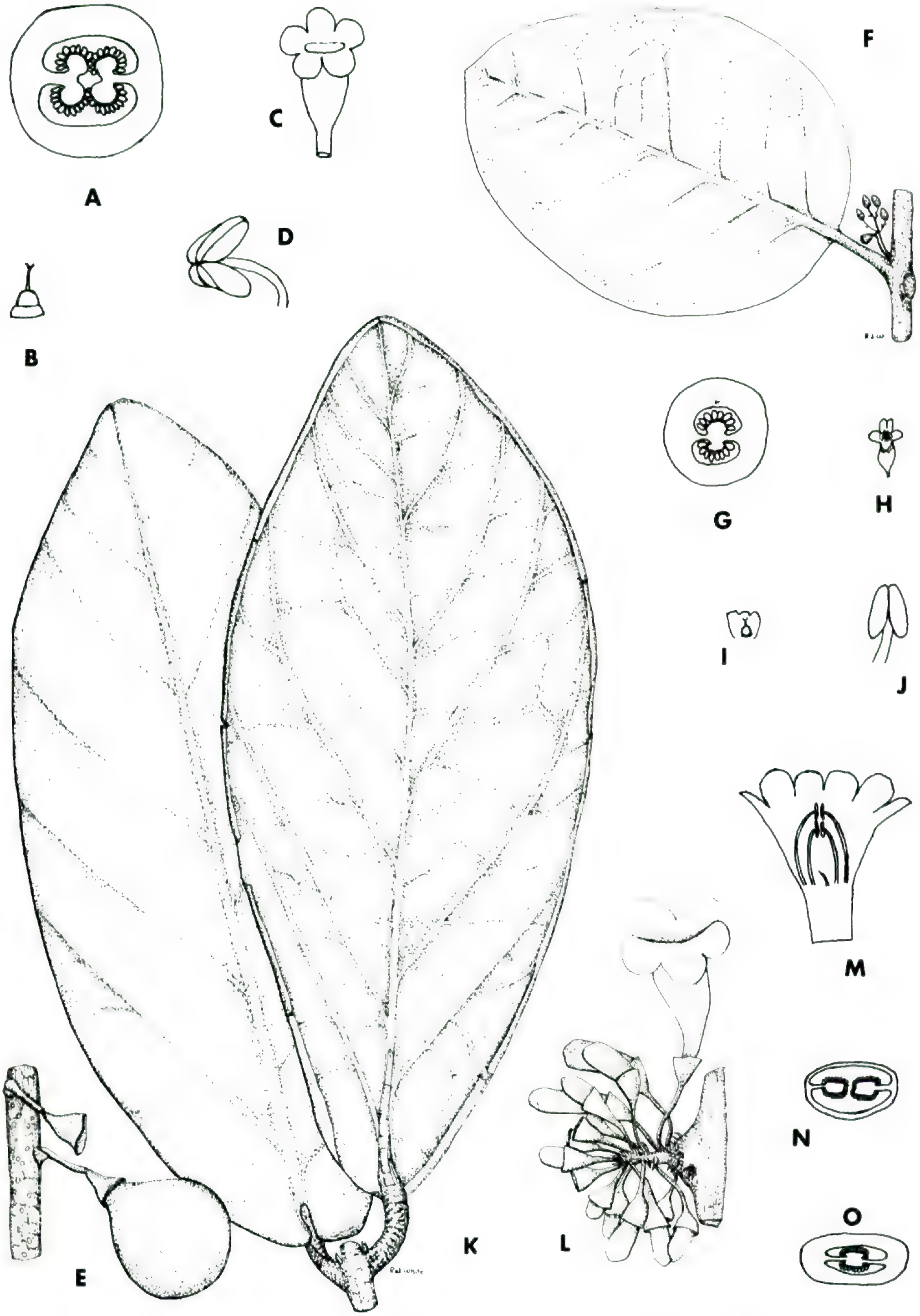


FIGURE 32. *Schlegelia*.—A–E. *S. nicaraguensis* Standl.—A. Ovary cross section (× 8).—B. Pistil and disc (× 1).—C. Corolla (× ½).—D. Anther (× 3½). [After *Gentry* 6545 (MO).]—E. Fruit (× ½). [After *Lewis et al.* 5248 (MO).]—F–J. *S. fuscata* A. Gentry.—F. Habit (× ½).—G. Ovary cross section (× 6).—H. Flower (× ½).—I. Pistil (× ½).—J. Anther (× 5). [After *Gentry* 2875 (MO).]—K–O. *S. dressleri* A. Gentry.—K. Leaves

CANAL ZONE: Ancon Hill across from Governor's House, *Croat 15026* (MO); *Gentry 1474B* (MO), *6049* (MO).

32. SCHEGELIA

Schlegelia Miq., Bot. Zeitung (Berlin) 2: 785. 1844. TYPE: S. *lilacina* Miq. = S. *violacea* (Aubl.) Griseb.

Dermatocalyx Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1855: 29. 1856. TYPE: *D. parviflorus* Oerst. = *Schlegelia parviflora* (Oerst.) Monachino.

Vines or scandent shrubs, sometimes epiphytic; stems without anomalous vasculature; branchlets more or less terete without interpetiolar glandular fields; pseudostipules small, blunt-conical or subulate, more or less appressed against the branchlet. *Leaves* simple, opposite, often strikingly coriaceous. *Inflorescence* an axillary raceme or a terminal or axillary (usually narrow) panicle, often conspicuously bracteate. *Flowers* with the calyx cupular, truncate or irregularly lobed; corolla white to pink, purple or red (or ?yellowish), tubular-campanulate to narrowly tubular, often short, more or less glabrous outside, conspicuously glandular lepidote on lobes inside; anthers glabrous, the thecae relatively short and thick, divaricate; pollen grains 3-colpate, the exine finely reticulate; ovary globose, bilocular with a single central placenta in each locule, the ovules multiseriate on each placenta, sometimes apically unilocular, the ovules then parietal on 2 bifid placentae fused lower in ovary. *Fruit* usually a spherical berry with a thin crustaceous pericarp, the lower part sheathed by the persistent calyx, more or less ellipsoid and hard-shelled in some species; seeds small, angular, wingless, surrounded by pulp.

About a dozen species (after the recent segregation of the genus *Gibsoniothamnus*) of tropical America ranging from Guatemala and the West Indies to Brazil.

Schlegelia is a confusing genus intermediate between the Bignoniaceae and Scrophulariaceae. I have accepted its traditional placement in the Bignoniaceae with some reservation. Williams (1970) recently described *Gibsoniothamnus*, a new genus of Scrophulariaceae which he interprets correctly as an additional link between that family and *Schlegelia*, and also proposed transfer of *Schlegelia* itself to Scrophulariaceae. The discovery of S. *dressleri*, the most bignoniaceous-looking species of *Schlegelia* yet described, provides an additional link between this genus and Bignoniaceae. *Schlegelia* species fall into two groups which may prove to be separate genera, one in the Bignoniaceae and one in the Scrophulariaceae. One group, closely allied with Bignoniaceae, has relatively large flowers and, in the two species where fruit is known, a hard-shelled, *Crescentia*-like fruit. The second group, more closely related to Scrophulariaceae, has species with small flowers and baccate fruits with only a crustaceous pericarp.

←

(× 3/10). [After *Dressler & Maas s.n.* (MO).]—L. Inflorescence (× ½).—M. Corolla split open (× ½).—N. Ovary cross section near apex (× 2½).—O. Ovary cross section near middle (× 2½). [After *Dressler 3507* (MO).]

One other species may occur in Panama. *Schlegelia darienensis* Seem. has been collected in the adjacent Choco of Colombia. It is recognized by its terminal inflorescence with leaf-like bracts.

Useful reference:

Williams, L. O. An overlooked genus of the Scrophulariaceae. Fieldiana, Bot. 32: 211–214. 1970.

a. Corolla large (more than 3.9 cm long and 1.1 cm wide at the mouth of the tube), tubular-campanulate; fruit ca. 4 cm in diameter (where known).
  b. Inflorescence a densely contracted, many-flowered raceme subtended by a conspicuous fascicle of basal bracts; leaves coriaceous, somewhat bullate, more than 30 cm long ..... 1. S. *dressleri*
  bb. Inflorescence a few-flowered axillary fascicle without a conspicuous fascicle of basal bracts; leaves chartaceous to subcoriaceous, not bullate, less than 12 cm long ..... 3. S. *nicaraguensis*
aa. Corolla small (less than 2.5 cm long and 0.5 cm wide at the mouth of the tube), tubular or shortly campanulate; fruit less than 1.5 cm in diameter.
  c. Corolla narrowly tubular with minute (1–2 mm long) non-reflexed lobes, more than 2 cm long; inflorescence a congested, densely branched, contracted, fastigiate panicle, each branchlet short, thick, and conspicuously jointed ..... 5. S. *sulfurea*
  cc. Corolla shortly tubular with larger (3–6 mm long) reflexed lobes, less than 1.3 cm long; inflorescence less-branched, not fastigiate, its branchlets not conspicuously thickened nor jointed.
    d. Inflorescence an open, unbranched raceme, sometimes a short, 3-flowered side branch replacing the lowest flower on each side; leaves drying a dark grayish brown ..... 2. S. *fuscata*
    dd. Inflorescence a more or less contracted panicle, sometimes almost fasciculate; most leaves drying olive to olive brown ..... 4. S. *parviflora*

1. **Schlegelia dressleri** A. Gentry.[6] TYPE: Panama, La Eneida near Cerro Jefe, *Dressler 3507* (MO, holotype; PMA, isotype).—FIG. 32K–O.

Vine, the stem without phloem arms in cross section; branchlets terete, rough-barked, lenticellate, without interpetiolar ridges or glandular fields. *Leaves* opposite or ternate, simple, elliptic, rounded at both ends, 30–45 cm long and 11–20 cm wide, extremely coriaceous, bullate, secondary veins 6–7 on a side, the main veins impressed above, conspicuously raised beneath, densely minute lepidote above and beneath, otherwise glabrous, with plate-shaped glands near base of the midvein beneath, drying olive, the petiole 2.4–3 cm long, lepidote, rough-barked. *Inflorescence* to 20-flowered, a contracted raceme 2–2.5 cm long subtended by a fascicle of subulate basal bracts, borne on older stems, the rachis and pedicels more or less lepidote and puberulous, each pedicel subtended by a light-drying subulate bract, 2–5 mm long, the pedicels 1.2–2.2 cm long. *Flowers* with the calyx cupular, truncate, 9–14 mm long and

[6] *Schlegelia dressleri* A. Gentry, sp. nov. Frutex scandens, ramulis subteretibus cortice suberoso, sine consociebus glandularum in nodis inter petioles; folia opposita vel ternata, elliptica, amplissima, percoriacea, bullata; inflorescentia floribus in racemis bracteatis contractis, fasciculo bractearum basalium subtenta; calyx cupulatus, truncatus, glaber; corolla albida, tubulo-campanulata; stamina didynama, thecis divergentibus; ovarium globosum, placentis duabus parietalibus apice, supra medium connatis, ovulis in utroque locule multiseriatis; fructus ignotus.

9.0–13 mm wide, drying dark brown, glabrous with scattered plate-shaped glands; corolla white, tubular-campanulate, 5.4–6.2 cm long and 1.4–1.8 cm wide at the mouth, the tube 4.3–4.8 cm long, the lobes 0.8–1.1 cm long, minutely lepidote outside near the base, otherwise glabrous, inside the lobes glabrous apically, becoming pubescent near the base with glandular lepidote trichomes merging into the glandular-puberulous trichomes of the upper third of the tube, lower part of the tube glabrous except for simple, multicellular, gland-tipped trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divergent, 3 mm long and 1.5–2.0 mm wide, the longer filaments 2.6–2.7 cm long, shorter filaments 2.0–2.1 cm long, the staminode 5 mm long, inserted 18–19 mm from the base of the tube; pistil 0.9 cm long, the ovary globose, 6 mm long and 6–7 mm wide, inconspicuously puberulous, the ovules multiseriate on 2 stalked parietal placentae in the upper 1 mm of ovary, these fused below so placentation is mostly axile with a single parietal placenta in each locule. *Fruit* unknown.

Apparently endemic to the Cordillera de San Blas of eastern Panama, S. *dressleri* has been collected only east of Cerro Jefe, Panama Province. This striking plant is the most distinctive species of the genus; its giant, leathery, somewhat bullate leaves are unmistakable. Its corolla is also the largest in *Schlegelia*. To date it is known only from two vines in a region fast being cleared by campesino squatters. It was in flower in March (1973) and late May (1968).

PANAMÁ: La Eneida, region of Cerro Jefe, *Dressler 3507* (MO, PMA). Campo Tres, 3 mi. NE of Altos de Pacora, *Liesner 565* (MO).

2. **Schlegelia fuscata** A. Gentry.[7] TYPE: Panama, Cerro Jefe, *Gentry 2875* (MO).—FIG. 32F–J.

Vine ("epiphyte," *Tyson et al. 3195*) to at least 2 cm in diameter, the bark dark, indistinctly ridged; stem without phloem arms in cross section; branchlets terete, scattered lepidote, without interpetiolar ridges or glandular fields. *Leaves* opposite, simple, elliptic, apically rounded, basally truncate to wide-cuneate, 7.6–12.6 cm long and 4.2–9.5 cm wide, extremely coriaceous, secondary veins 4–5 on a side, the main veins impressed above, raised beneath, lepidote above and beneath, otherwise glabrous, the lepidote trichomes glandular and congested at the base of blade beneath, this glandular area usually black from infection by a member of the Melanconiales (fungus), when fresh glossy green above and dull pale green beneath, drying brown above and beneath, the petiole 1.3–2.5 cm long. *Inflorescence* a 5–12-flowered axillary raceme or a subpanicle with the basal pedicels of the raceme forked and bearing 2 flowers,

[7] *Schlegelia fuscata* A. Gentry, sp. nov. Frutex scandens; folia opposita, elliptica, percoriacea, in sicco fusca; inflorescentia floribus 6–12, in racemis laxis vel paniculiformis pedicellis basilaribus furcatis ferentibus duos vel tres flores, bracteis minimis inconspicuis; calyx cupulatus, plus minusve vadose lobatus, glabrus vel leviter lepidotus, margine pubescenti; corolla tubo albo, lobis roseis, tubulosa lobis refractis; stamina didynama, thecis non divergentibus; ovarium globosum, ovulis multiseriatis, in placenta singulari ad centrum utriusque loculi; fructus globosus, ad 1.2 cm diam., calyce persistenti.

the branches simple-pubescent, each pedicel pair and each flower subtended by a pair of acute bracts with ciliate tips, the rachis 1.2–5 cm long, pedicels 4–8 mm long. *Flowers* with the calyx cupular, widest at the middle, with 4–5 round-tipped lobes, 6–7 mm long and 1–6 mm wide, glistening white with a slight pink tint when fresh, black when dry, inconspicuously lepidote, simple-pubescent at the tips; corolla greenish-white on the tube outside, the lobes pink, paler at the tips and deeper at the base shading into the purplish-pink of the throat, tubular with reflexed lobes, 1.0–1.1 cm long and 4 mm wide at the mouth, the tube 7 mm long, the lobes 3–4 mm long, the posterior pair sometimes partially fused, glabrous outside, the lobes glandular-lepidote to glandular-puberulent inside, the tube glabrous inside except for long simple multicellular glandular trichomes at the level of stamen insertion; stamens didynamous, the anther thecae not divergent, 1.5–2 mm long, the filaments all ca. 0.8 cm long but the posterior pair bent more sharply holding the posterior anthers lower in the throat, the staminode 3 mm long, inserted 4–5 mm from the base of the tube; pistil 5 mm long, the ovary spherical, 2–2.5 mm long and 2.5–3.0 mm wide, glabrous, the ovules 8–9-seriate on a single central placenta in each locule; disc absent. *Fruit* a spherical fleshy berry to 1.2 cm in diameter, pale purple when fresh, the calyx persistent and covering the lower half to third of the fruit, glabrous but large-papillate; seeds angular, papillate-surfaced, 2–3 mm long, less than 1 mm wide.

This species is only known from the Cerro Jefe and Santa Rita Ridge regions of central Panama in the tropical wet forest and premontane rain forest at an elevation of 800 to 1000 m, where it has been collected a number of times. *Schlegelia fuscata* is closest to S. *parviflora*, differing most conspicuously in its open, more or less racemose inflorescence which is unbranched or with a single short, basal, 3-flowered side branch on each side and in its uniformly dark-drying, extremely coriaceous leaves. The leaves are always conspicuously blackened below in the glandular area at the base of blade, presumably from a fungal infection.

This species may be no more than a local form of the heterogeneous S. *parviflora*, but on the basis of present evidence it is different enough to be considered specifically distinct.

COLÓN: Santa Rita Ridge, *Dressler 3618* (PMA). PANAMÁ: Cerro Jefe summit, *Dwyer et al. 7276* (MO); *Gentry 2875* (MO), *3692* (MO); *Tyson et al. 3195, 4363, 5304* (all SCZ).

3. **Schlegelia nicaraguensis** Standl., Trop. Woods 16: 44. 1928. TYPE: Nicaragua, Bluefields, *Englesing 99* (F, GH, K).—FIG. 32A–E.

Woody *vine*, stem without phloem arms in cross section; branchlets lepidote, sparsely pubescent at least at the nodes, without interpetiolar ridges or glandular fields, pseudostipules subulate, to 3 mm long, pubescent. *Leaves* opposite, simple, elliptic-obovate, apically rounded or apiculate, basally wide cuneate, usually abruptly short-attenuate, 7.6–11 cm long and 3.8–7.4 cm wide, chartaceous to rigid-chartaceous, the secondary veins 5–8 on a side, raised above, the midvein impressed above, all main veins raised beneath, the midvein

conspicuously so, inconspicuously lepidote (often deciduously) above and beneath, sparsely puberulous along main veins beneath, otherwise glabrous, plate-shaped glands scattered over the leaf surface beneath, congested at the base of the blade, each gland surrounded by a raised epidermal papilla, drying brown to gray brown, petiole 0.8–1.6 cm long, slightly lepidote, flat-topped, inconspicuously puberulous along the angles. *Inflorescence* a few-flowered, axillary fascicle on older branchlets below the leaves, the pedicels puberulous. *Flowers* with the calyx cupular, truncate to slightly lobed, 1 cm long and 1 cm wide, when fresh violet with white spots, dark brown when dry, lepidote, puberulous mostly near rim and base with immersed plate-shaped glands mostly toward the apex; corolla cream or yellowish at base, the lobes magenta, tubular-campanulate, 3.9–4.7 cm long and 1.1–2.1 cm wide at the mouth, the tube 3.1–3.7 cm long, the lobes 0.5–0.8 cm long, glabrous outside and at the tips inside, lepidote near the middle and base, the pubescence merging into the simple multicellular trichomes of the upper third of the tube, lower part of tube glabrous except for simple gland-tipped trichomes at the level of stamen insertion; stamens didynamous, the anther thecae thick, slightly divergent, 3 mm long and 1.5–2.0 mm wide, longer filaments 2.0–2.2 cm long, shorter filaments 1.5–1.7 cm long, staminode 3–5 mm long, inserted 5 mm from base of corolla tube; pistil 0.5–0.7 cm long, the ovary truncately spherical, glabrous, 3 mm long and 3 mm wide, the ovules multiseriate on 2 bifid, stalked, parietal placentae in upper ⅔ of ovary, these fused in the lower third and placentation axile with a single central placenta in each locule; disc thin, sunken into the base of the ovary. *Fruit* spherical, hard-shelled, glabrous, ca. 4 cm in diameter, subtended by the persistent calyx, the seeds small, angular, 2–3 mm long and 1 mm wide, borne on an incompletely fused septum.

Previously known only from Nicaragua and Guatemala, the Panamanian collections from the Cerro Jefe and Santa Rita regions of eastern Panama extend the range of this species the length of Central America. It is evidently restricted to the poorly known tropical wet forest. The species has been collected in flower in December, January, and June in Panama, indicating an irregular flowering season.

Schlegelia nicaraguensis is distinguishable from most species of the genus by its large (ca. 4 cm long) corolla. It differs from S. *dressleri* most strikingly in its much smaller leaves. This species is closely related to S. *parasitica* of the West Indies and might prove to be a variety of that species.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1051* (GH, MO). COLÓN: Santa Rita Ridge, *Croat 13201* (MO, SCZ), *14188* (MO); *Gentry 6545* (MO); *Lewis et al. 5248* (MO). PANAMÁ: Altos del Río Pacora, *Lewis et al. 2319* (MO, SCZ).

4. **Schlegelia parviflora** (Oerst.) Monachino, Phytologia 3: 103. 1949.

Dermatocalyx parviflorus Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1855: 28: 1856. TYPE: Costa Rica, Alajuela, *Oersted s.n.* (not seen; illustration in type herbarium at C).

Citharexylum ramizii Glaziou, Bull. Soc. Bot. France 58, Mém. 3: 545. 1911, nomen nudum.

Tabebuia micrantha Kränzl., Fedde Repert. 17: 215. 1921. TYPE: Brazil, São Paulo, *Mosén 3662* (not seen; K, photo).
Schlegelia ramizii Sandw., Kew Bull. 1930: 211. 1930. TYPE: Brazil, Rio de Janeiro, *Glaziou 15327* (C, K).
Aegiphila congesta Standl. *ex* Moldenke, Brittonia 1: 471. 1934, nomen nudum.
Schlegelia ramizii var. *costaricensis* Sandw., Kew Bull. 1940: 303. 1941. TYPE: Costa Rica, San José, *Skutch 4125* (A, K, MO).
S. *ramizii* var. *macrandra* Sandw., Kew Bull. 1940: 303. 1941. TYPE: Peru, Loreto, *Klug 2340* (K).
S. *ramizii* var. *trichandra* Sandw., Kew Bull. 1940: 304. 1941. TYPE: British Honduras, *Peck 666* (K).
S. *roseiflora* Ducke, Trop. Woods 76: 29. 1943. TYPE: Brazil, Amazonas, *Ducke 1142* (MO, NY, US).
S. *organensis* Kuhlm., Rodriguesia 20: 7, *pl. 1.* 1946. TYPE: Brazil, Rio de Janeiro, *Kuhlmann s.n.* (not seen).
S. *macrophylla* Ducke, Trop. Woods 90: 29. 1946. TYPE: Brazil, Amazonas, *Ducke 1854* (K, NY, US).
S. *gentlei* Lundell, Wrightia 4: 95. 1968. TYPE: Guatemala, Alta Verapaz, *Contreras 4471* (US).

Woody *vine*; stem without phloem arms in cross section; branchlets terete, glabrous, without interpetiolar ridges or glandular fields. *Leaves* opposite, simple, obovate to elliptic-obovate, apically rounded to acute, basally cuneate, 11.2–19.5 cm long and 4.8–14.7 cm wide, coriaceous, secondary veins 6–8 on a side, minutely lepidote at least beneath, otherwise glabrous with a glandular field near the base of the blade below, drying olive to olive brown, the petiole 1.0–2.4 cm long. *Inflorescence* a few- to many-flowered axillary, more or less contracted, sometimes almost fasciculate panicle, the branches puberulous with small bracts, 1–2 mm long, subtending many of its dichotomies, these more or less short-puberulous at least along the margins. *Flowers* with the calyx cupular with 2–3 round-tipped lobes, 4–6 mm long and 3–5 mm wide, inconspicuously lepidote or subpuberulous at least at the base, usually drying tan; corolla white or cream flushed with pink, tubular with reflexed lobes, 1.0–1.2 cm long and 0.4 cm wide at the mouth, the tube 0.6–0.8 cm long, the lobes 0.4–0.6 cm long, glabrous outside, the lobes glandular-lepidote to glandular-puberulous inside, the tube scattered pubescent in the upper half inside, glabrous below the level of stamen insertion; stamens more or less equal, the anther thecae thick, slightly divergent, 1 mm long and almost 1 mm wide, the filaments 4 mm long, the bases swollen and pubescent, the staminode 2–3 mm long, inserted 4 mm from the base of the corolla tube; pistil 3–4 mm long, the ovary spherical, 1.5–2 mm long and 2 mm wide, glabrous, the ovules multi-(ca. 8-)seriate on a central placenta in each locule; disc absent. *Fruit* a spherical, fleshy berry, 0.9–1.1 cm in diameter, glabrous, the lower part covered by the persistent calyx; seeds angular, ca. 2 mm long, less than 1 mm wide.

One of the most-collected species of the genus, S. *parviflora* occurs in the tropical wet forest and premontane wet forest from Guatemala and British Honduras to Brazil. In addition to the listed synonyms, a number of manuscript names have been used for various collections of S. *parviflora*.

The species is characterized vegetatively by its stiff coriaceous leaves, much smaller than those of S. *dressleri*. They differ from the round-tipped leaves of S. *fuscata* in being usually more or less subacuminate and from the elliptic-

oblong leaves of S. *sulfurea* in being more or less obovate. In flower or fruit S. *parviflora* differs from the likewise small-flowered S. *fuscata* by its fasciculate or paniculate inflorescence as compared with the open, few-branched racemose or subpaniculate inflorescence of the latter.

Schlegelia parviflora is extremely variable as here interpreted, but understanding of its variation has so far proved difficult. It seems best to follow Sandwith (in herb.) in using the name in a relatively wide sense until a thorough revision of the genus is possible.

A confusing collection is *von Hagen & von Hagen 2122* (NY) from Chiriquí, Panama, which is intermediate between S. *monachinoi* Moldenke and S. *parviflora*. It was determined by Moldenke as S. *monachinoi* of Colombia, a taxon of uncertain status.

BOCAS DEL TORO: Río Teribe between Quebrada Treglo and Puerto Palenque, *Kirkbride & Duke 538* (MO, SCZ). COLÓN: Santa Rita Ridge, *Correa & Dressler 747* (MO, PMA, SCZ). DARIÉN: Camp Summit, *Duke 15486* (MO). PANAMÁ: Along road from Cerro Azul to Cerro Jefe, *Tyson 5304* (SCZ). WITHOUT LOCALITY: *Seemann 66* (BM).

5. **Schlegelia sulfurea** Diels, Notizbl. Bot. Gart. Berlin 14: 39. 1938. TYPE: Ecuador, *Schultze-Rhonhof 1927* (not seen).

S. *fastigiata* Schery, Ann. Missouri Bot. Gard. 29: 367. 1942. TYPE: Panama, Bocas del Toro, *von Wedel 773* (GH, MO, US).

Woody *vine*; stem without phloem arms in cross section; branchlets terete, glabrous or inconspicuously short puberulous, without interpetiolar ridges or glandular fields; pseudostipules lanceolate, acute, paired, appressed against the branchlet. *Leaves* opposite, simple, elliptic-lanceolate to narrowly elliptic, acute to short-acuminate, basally broadly cuneate to truncate, 10–33 cm long and 4–13.2 cm wide, chartaceous, to rigid-chartaceous, secondary veins 7–12 on a side, veins slightly raised above, conspicuously so beneath, essentially glabrous above and beneath with some plate-shaped glands beneath, these concentrated at the base of the blade, drying dark olive beneath, blackish above, the petiole usually thick, often woody, slightly winged apically from the more or less attenuate leaf blade, flat or shallowly grooved above, convex beneath, 0.5–1.5 cm long. *Inflorescence* a congested, extremely densely branched, contracted panicle, the branchlets short and conspicuously jointed, woody, usually shortly puberulous. *Flowers* with the calyx cupular, truncate, 5–8 mm long and 5–7 mm wide, glabrous to slightly lepidote or puberulous, pink when fresh, drying dark red; corolla creamy white with pink tip (*Porter et al. 4432*), narrow-tubular, the lobes small and not reflexed, 2.0–2.5 cm long and 0.3–0.4 cm wide at the mouth of tube, the tube 1.9–2.4 cm long, the lobes 1–2 mm long, the tube glabrous inside and out, the lobes slightly glandular-lepidote outside, the anther thecae slightly divergent, each 1–1.5 mm long and ca. 1 mm thick, the longer filaments 0.9–1.0 cm long, shorter filaments 0.8–0.9 cm long, puberulous at the base, the staminode 3 mm long, inserted 10–12 mm from the base of the tube; pistil 4 cm long, the ovary spherical, lepidote, 2 mm long and 2 mm wide, the ovules multi-seriate in each locule on a single central placenta; disc cupular-

pulvinate, somewhat sunken into the base of the ovary, 1 mm long and 2.5 mm wide. *Fruit* a berry, spherical, 1.0–1.4 cm long and 1.3–1.5 cm wide, its lower quarter covered by the expanded persistent calyx, glabrous.

This is a plant of the tropical wet forest. It ranges from Guatemala to Ecuador at altitudes from sea level to almost 1000 m.

The type of S. *sulfurea* was destroyed at Berlin, but other specimens from the type locality in Ecuador are clearly the same as S. *fastigiata*. I have seen a duplicate of the Ruiz and Pavon collection which was mentioned in the original description of S. *sulfurea* and it, too, is conspecific with the plant formerly known as S. *fastigiata*.

The relatively long, narrow leaves and subulate-appressed pseudostipules are good recognition characters, and the inflorescence is distinctive. *Schlegelia darienensis* is known from just across the Colombian border and might be expected to occur in Panama. It has somewhat similar fastigiate branches in its inflorescence but this inflorescence differs in being terminal, elongate, and having conspicuous leaf-like bracts.

BOCAS DEL TORO: Region of Almirante, *Cooper 167* (F, NY, US), *169*, *169A* (both F). Cerro Bonyic above Quebrada Hurón, *Kirkbride & Duke 600* (MO). Isla Colón, *von Wedel 44* (GH, MO). Vicinity of Chiriquí Lagoon, *von Wedel 154* (MO, US), *1397* (GH, MO, US). Water Valley, *von Wedel 773*, *1447* (both GH, MO, US), *1468* (GH, MO), *1659* (GH, MO, US). Old Bank Island, *von Wedel 2126* (GH, MO, NY, US). Fish Creek mountains, *von Wedel 2361* (MO). Fish Creek lowlands, *von Wedel 2375* (MO). Fish Creek Hills, *von Wedel 2419* (GH, MO, US). COCLÉ: Summit of Cerro Pilón above El Valle de Antón, *Dwyer et al. 4503* (MO, SCZ); *Dwyer & Lallathin 8691* (MO). 2 mi. N of Cerro Pilón, *Liesner 729* (MO). Foot of Cerro Pilón, *Porter et al. 4432* (MO). DARIÉN: Along Sea Level Canal Route 17, *Oliver et al. 3707* (MO); *Duke 15491* (MO). PANAMÁ: N of El Llano, *Gentry 5086* (MO). SAN BLAS: Headwaters of Río Cuadi (drill site 22), *Duke et al. 3635* (MO). VERAGUAS: Along Río Primero Brazo ca. 5 mi. NW of Santa Fé, *Croat 23127* (MO); *Liesner 1000* (MO).

33. SCOBINARIA

Scobinaria Seib., Carnegie Inst. Washington Publ. 527: 408. 1940. TYPE: S. *verrucosa* (Standl.) Seib. = S. *japurensis* (DC.) Sandw.

Lianas; stems with 4 phloem arms in cross section; branchlets terete with interpetiolar glandular fields, these usually sharply limited above by a more or less V-shaped line connecting opposite petioles; pseudostipules small and inconspicuous. *Leaves* 2-foliolate, often with a simple tendril. *Inflorescence* a few-flowered axillary or terminal panicle. *Flowers* with the calyx large and thin, campanulate, bilabiate, variously lepidote at least at the base; corolla lavender to magenta, tubular-campanulate, puberulous outside; anthers glabrous, the thecae straight, divergent; pollen grains 3-colpate; ovary linear-tetragonal, finely lepidote-papillate, the ovules 2-seriate in each locule. *Fruit* a compressed linear-oblong capsule, the valves parallel to the septum, verrucose tuberculate, drying black, the median nerve not visible; the seeds thin, bialate, the wings mostly brown, hyaline at the extreme margin, not demarcated from the seed body.

Probably with only one species, the genus is often included with *Arrabidaea*. It occurs in continental tropical America, ranging from southern Mexico to Amazonia.

1. **Scobinaria japurensis** (DC.) Sandw., Kew Bull. 13: 440. 1959.—Fig. 33.

Adenocalymma japurense Mart. *ex* DC., Prodr. 9: 203. 1845, pro syn.
Phryganocydia japurensis Mart. *ex* DC., Prodr. 9: 214. 1845, pro syn.
Tabebuia japurensis DC., Prodr. 9: 214. 1845. TYPE: Brazil, Amazonas, *Martius s.n.* (M; G-DC, fragment).
Arrabidaea japurensis (DC.) Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 65. 1896.
A. lenticellosa Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 64. 1896. TYPE: Brazil, Matto Grosso, *Riedel 1469* (K).
A. oligantha Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 64. 1896. TYPE: Brazil, *Gardner 1258* (K, as *Hostmann 1258* from Surinam).
Paragonia schumanniana Loes., Bot. Jahrb. Syst. 23: 130. 1897. TYPE: Nicaragua, Matagalpa, *Rothschuh 230* (not seen).
Arrabidaea nicotianaeflora Kränzl., Notizbl. Bot. Gart. Berlin 6: 369. 1915. TYPE: Brazil, Rio Acre, *Ule 9782* (K).
Adenocalymma verrucosum Standl., Publ. Field Columbian Mus., Bot. Ser. 4: 323. 1929. TYPE: Honduras, Atlantida, *Standley 54891* (A, F, US).
Arrabidaea belizensis Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 48. 1930. TYPE: British Honduras, Middlesex, *Schipp 284* (BM, F, K, MO, NY, US).
Martinella verrucosa (Standl.) Standl., Contr. Arnold Arbor. 5: 138. 1933.
Scobinaria verrucosa (Standl.) Seib., Carnegie Inst. Washington Publ. 522: 408. 1940.
S. amethystina Dugand, Caldasia 7(31): 24. 1955. TYPE: Colombia, Bolivar, *Romero-Castañeda 1735* (COL).

Liana to at least 10 cm in diameter, the bark gray and conspicuously orange-lenticellate; stem with 4 phloem arms in cross section; branchlets variable, subtetragonal to subterete, more or less longitudinally striate, glabrous to lepidote or puberulous, brownish when fresh, the nodes normally with interpetiolar glandular fields sharply limited above by a more or less V-shaped line connecting opposite petioles; pseudostipules lacking. *Leaves* 2-foliolate, sometimes with a tendril; leaflets more or less ovate, acuminate to obtuse, rounded to broadly cuneate, 5.2–17 cm long and 2.4–11.8 cm wide, chartaceous to membranaceous, secondary veins (3–)4–6 on a side, the basal pair usually not parallel to the others, scattered lepidote especially on the veins, pubescent beneath with long simple trichomes in leaf axils and sometimes along the base of the main veins, above usually minutely puberulous at the base of the midvein, usually drying greenish-olive with reddish veins and veinlets beneath; tendril simple, 8–20 cm long; petiolules 1.0–4.2 cm long, petiole 1.3–5.1 cm long, lepidote and puberulous at least above. *Inflorescence* a few-flowered axillary panicle, the branches lepidote, each pedicel subtended by a bract and with 2 bracteoles, these minute, subulate, ciliate. *Flowers* with sweet slightly spicy aroma, the calyx tubular-campanulate, strongly bilabiate, membranaceous, 1.8–2.4 cm long and 0.8–1.2 cm wide, white when fresh, strongly lepidote or lepidote only at the base; corolla lavender to magenta with a white throat, tubular-campanulate, 4.5–7.9 cm long and 1.1–2.1 cm wide at the mouth, the tube 3.2–5.7 cm long, lobes 0.7–1.8 cm long, pubescent outside with simple multicellular trichomes, the lobes ciliate-fringed and pubescent, the tube mostly glabrous inside, pubescent at the level of stamen insertion; stamens didynamous,

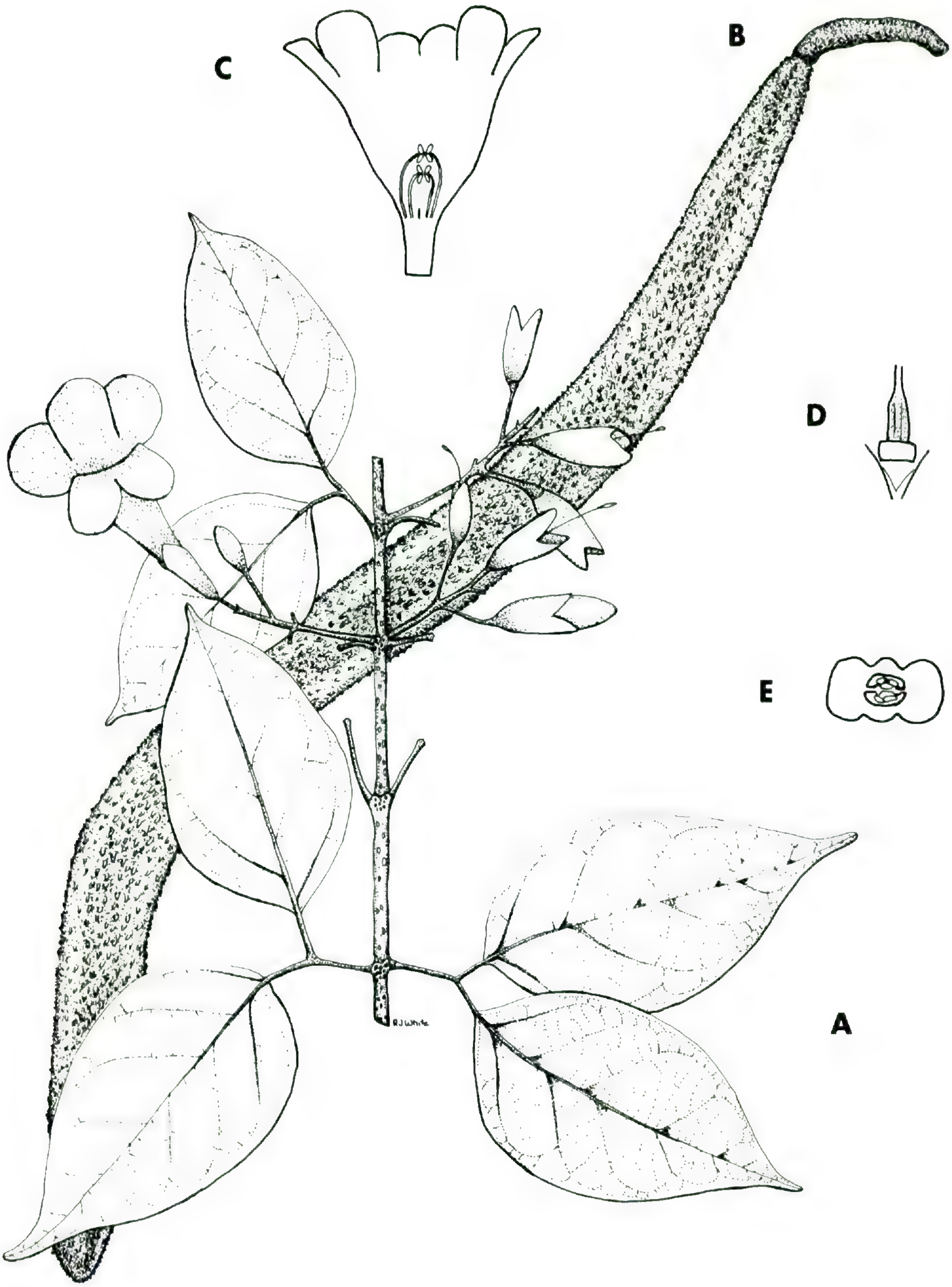


FIGURE 33. *Scobinaria japurensis* (DC.) Sandw.—A. Habit (× ½). [After *Gentry 6267* (MO).]—B. Fruit (× ½). [After *Gentry 4185* (MO).]—C. Corolla split open (× ½). —D. Ovary and disc (× 1½).—E. Ovary cross section (× 7½). [After *Gentry & Dwyer 5509* (MO).]

the anther thecae divaricate, 3 mm long, the longer filaments 1.7–2.0 cm long, shorter filaments 1.1–1.4 cm long, the staminode 1–3 mm long, inserted 1.2–1.4 mm from base of corolla tube; pistil 2.5–2.8 cm long, the ovary linear-oblong, more or less tetragonal, 3 mm long and 1–1.5 mm wide, densely lepidote, minutely papillate, the ovules 2-seriate in each locule; disc annular pulvinate, 1 mm long and 2.5 mm wide. *Capsule* linear, acute to obtuse, flattened, 12–46 cm long and 1.3–2.5 cm wide, the surface black, conspicuously verrucose-tuberculate, sometimes lepidote between tubercles, the tubercles sometimes short and little more than papillae; seeds 1.2–1.8 cm long and 3.9–5.1 cm wide, the wings membranaceous, brown, sometimes with the extreme margin hyaline, not well demarcated from the seed body.

A common but infrequently collected vine of the tropical wet forest, this species also occurs less frequently in premontane wet forest and tropical moist forest. It ranges from British Honduras to Venezuela and Boliva. The species flowers during the wet season from June to November. Seed release is during the dry season.

Recognition of sterile vines in the field is by a combination of characters. In general S. *japurensis* has interpetiolar glandular fields with a distinct and often centrally notched interpetiolar ridge forming an upper margin. The bark of mature plants is grayish with distinctive orange lenticels. The lower lateral nerve pair of the leaflets tends to ascend arcuately in contrast to the other lateral nerves. However, any combination of these characteristics seems possible, especially in young plants, making this species difficult to identify when sterile. The linear, verrucose-tuberculate fruit is unique and resembles a wood rasp in texture. Some specimens have the tubercles much more accentuated than others, but this is of no taxonomic significance. The flower with its flattened tube and large, bilabiate, membranaceous calyx is also distinctive.

Sandwith (Kew Bull. 22:403–420. 1968) reunited *Scobinaria* with *Arrabidaea*, but it is sufficiently distinct to be retained, even if it should prove monotypic. The peculiar fruit and calyx, the small inflorescence, never 3-foliolate leaves, much thicker stem with a different type of bark, and especially the large, relatively thick-textured, dorsally compressed corolla all argue for its separation. Most of the series *Macrocalycinae* of *Arrabidaea* as constituted by Bureau and K. Schumann in *Flora Brasiliensis* is conspecific with S. *japurensis*. Although I have not included *A. egensis* Bur. & Schum. in the synonymy of *S. japurensis*, I suspect that it is probably a pubescence form; certainly it is a *Scobinaria* rather than an *Arrabidaea*.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 609* (F); *Croat 9040, 10129* (both MO), *13266* (MO, SCZ), *13983* (MO), *14102* (MO, SCZ), *14995, 15168* (both MO), *15564* (MO, SCZ); *Foster 1071* (PMA), *1387* (MO, PMA); *Gentry 709* (MO); *Kenoyer 532, 535* (both US); *Shattuck 438* (F, US), *903* (MO, US); *Starry 151* (F, MO); *Wetmore & Abbe 56* (F); *Woodworth & Vestal 324* (F). Las Cruces Trail in Madden Forest, *Gentry 1385* (MO). CHIRIQUÍ: 12 mi. N of Puerto Armuelles, *Croat 21965* (MO). 7.5 mi. W of Puerto Armuelles, *Croat 22486* (MO). COLÓN: Ridge W of Portobelo, *Gentry 1765* (MO). Río Guanche, *Gentry 6318* (MO). DARIÉN: Río Piñas, *Duke 10562* (MO). Río Balsas between Manene and Tusijuanda, *Duke 13562* (MO). Puerto Sta. Dorothea, *Dwyer 2236* (MO). S of Jaqué, *Gentry 4098* (MO). Río Jaqué upriver from Jaqué, *Gentry 4185* (MO).

Figure 34. *Spathodea campanulata* Beauv.—A. Habit (× ½). [After *Croat 8890* and *Gentry 700B* (both MO).]—B. Fruit and seed (× ½). [After *Croat s.n.* (MO).]

S of La Palma, *Gentry 4308* (MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4427* (MO). Trail to Cerro Pirre from village of Pirre, *Gentry 4779* (MO). PANAMÁ: Río Pasiga, *Gentry 2193, 2312* (both MO). Between Río Sulugandí and Río Espavé, *Gentry 4990* (MO). Junction of Ríos Pacora and Corso to headwaters of Río Corso, *Oliver 2359* (MO, SCZ). SAN

BLAS: Near stream above Puerto Obaldía, *Gentry 1536* (MO). Mainland opposite Playón Chico, *Gentry 6374* (MO). VERAGUAS: N of Santa Fé, *Gentry 3016* (MO).

34. SPATHODEA

Spathodea Beauvois, Fl. Oware 1: 46. 1805. LECTOTYPE: S. *campanulata* Beauvois.

Trees. *Leaves* imparipinnate, 9–10-foliolate. *Inflorescence* a terminal raceme, the lower pedicels longer. *Flowers* with the calyx large, spathaceous, narrowing to a recurved tip; corolla red-orange or crimson, usually with a yellow fringe, large, broadly campanulate above a cylindrical base, glabrous outside; anthers glabrous, the thecae divaricate; ovary narrowly oblong, the ovules multiseriate in each locule. *Fruit* a narrowly oblong-elliptic capsule, the valves keeled, narrowed at the ends, dehiscing perpendicularly to the septum; seeds flat, winged, the wings broad and hyaline-membranaceous.

A monotypic genus of tropical Africa.

1. **Spathodea campanulata** Beauvois, Fl. Oware 1: 47. *tab*. 27. 1805.—FIG. 34.

Tree to at least 25 m tall and 40 cm d.b.h. *Leaves* imparipinnate, usually 9–15-foliolate, the leaflets more or less elliptic, acute to acuminate, asymmetrically subtruncate or widely cuneate basally, subsessile, slightly puberulous along main veins. *Inflorescence* a terminal raceme, the lower pedicels longer and curving upward to give a flat-topped effect. *Flowers* with the calyx spathaceous tapering to a recurved point which bends away from the corolla, 4.5–5 cm long; corolla red-orange with a yellow border, broadly campanulate above a cylindrical base, large, 8.5–9.0 cm long and 4.5–5.0 cm wide at the mouth, the tube 6–6.5 cm long, the lobes 1.5–2 cm long, glabrous; stamens 4, subexserted, held against the floor of the tube, the anther thecae divaricate, slender, 8 mm long; ovary narrowly oblong, minutely papillate, the ovules multi-seriate in each locule. *Capsule* narrowly oblong-elliptic, dehiscing on one side, the valves boat-shaped, narrowing to the ends, 17–25 cm long and 3.5–7 cm broad; seeds thin, winged, the wings broad and hyaline-membranaceous, sharply demarcated.

A native of tropical Africa, S. *campanulata* is planted extensively as an ornamental and shade tree throughout the tropics. Its bright-colored, showy flowers are produced during most of the year and make it one of the most attractive and best known species of Bignoniaceae. In the neotropics it often sets fruit and at times is spontaneous though seldom naturalized. "African tulip tree."

CANAL ZONE: Barro Colorado Island, *Croat 5177, 8890* (both MO). Summit Garden, *Gentry 700B* (MO). Curundu, *Tyson 2042* (MO, SCZ).

35. STIZOPHYLLUM

Stizophyllum Miers, Proc. Roy. Hort. Soc. 3: 197. 1863. LECTOTYPE: S. *denticulatum* Miers = S. *perforatum* (Cham.) Miers.

Lianas; stems with 4 phloem arms in cross section, the extreme center mostly hollow; branchlets terete without interpetiolar glandular fields; pseudostipules inconspicuous or more or less spathulate and early deciduous. *Leaves* 3-foliolate, conspicuously pellucid-punctate from the lepidote-peltate glands on the lower surface, the terminal leaflet often replaced by a simple or trifid tendril. *Inflorescence* a few-flowered axillary raceme. *Flowers* with the calyx campanulate, sometimes more or less inflated, pubescent, irregularly shallowly bilabiate to 5-lobed; corolla white or cream, the lobes sometimes flushed with pink; anthers glabrous or pubescent on the margin of the thecal openings, the thecae straight, divaricate; pollen grains 3-colpate, the exine microreticulate; ovary linear-tetragonal, lepidote, the ovules 2-seriate in each locule. *Fruit* a narrow, linear capsule, the valves parallel to the septum, thin, convex, usually faintly striate and more or less pubescent; seeds thin, bialate, the wings membranaceous, brownish, weakly demarcated.

Probably three species in continental tropical America ranging from southern Mexico to Brazil.

Miers' *S. denticulatum* matches in every respect except foliaceous pseudostipules (which are ephemeral and inconstant in this genus) the genus described with it and is the logical choice as lectotype. Although Bureau and Schumann (1896) lump this species and all twelve of Miers' other species of the genus under *S. perforatum*, I am not sure of the correct interpretation of this group. Sandwith has suggested (Kew Bull. 1954: 608. 1955) that *Stizophyllum* might constitute a single highly variable species, and Macbride followed this suggestion in his treatment for *Flora of Peru* (Field Mus. Nat. Hist., Bot. Ser. 13(95): 56. 1961). I am convinced, however, that there are at least three species in the genus, and perhaps some other variants deserve infraspecific recognition.

Sterile plants of this genus can be readily identified in the field by the pellucid-punctate dots on their leaves (except when very young) and the conspicuously hollow stems. Fruits of the genus are among the narrowest in the family and are difficult to discern from twigs at any distance. The white flower color and slightly pubescent to glabrous anthers are also useful characters.

a. Branchlets and petiolules reddish hispid; tendrils trifid; calyx expanded-campanulate, membranaceous; fruit villous-pubescent ..... 1. *S. inaequilaterum*
aa. Branchlets and petiolules grayish or yellowish puberulous; tendrils simple; calyx short, campanulate, chartaceous; fruit short-puberulous ..... 2. *S. riparium*

1. **Stizophyllum inaequilaterum** Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 221. 1896. TYPE: Peru: Mayna, *Poeppig 1827* (W; B, destroyed).—FIG. 35A–B.

Bignonia inaequilatera Poeppig *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 222. 1896, pro syn., non Poeppig *ex* Bur., Addansonia 8: 289. 1868.
Cremastus rufo-villosus Herzog, Meded. Rijks-Herb. 29: 40. 1916. TYPE: Bolivia, Misiones de Guarayus, *Herzog 265*, 1st journey (L; K, photo).

Liana to at least 2.5 cm in diameter, the bark smooth, somewhat scaly, stem subtetragonal with hollow center and 4 phloem arms in cross section; branchlets terete, hollow, longitudinally striate, strongly pubescent with long (to 1.5 mm)

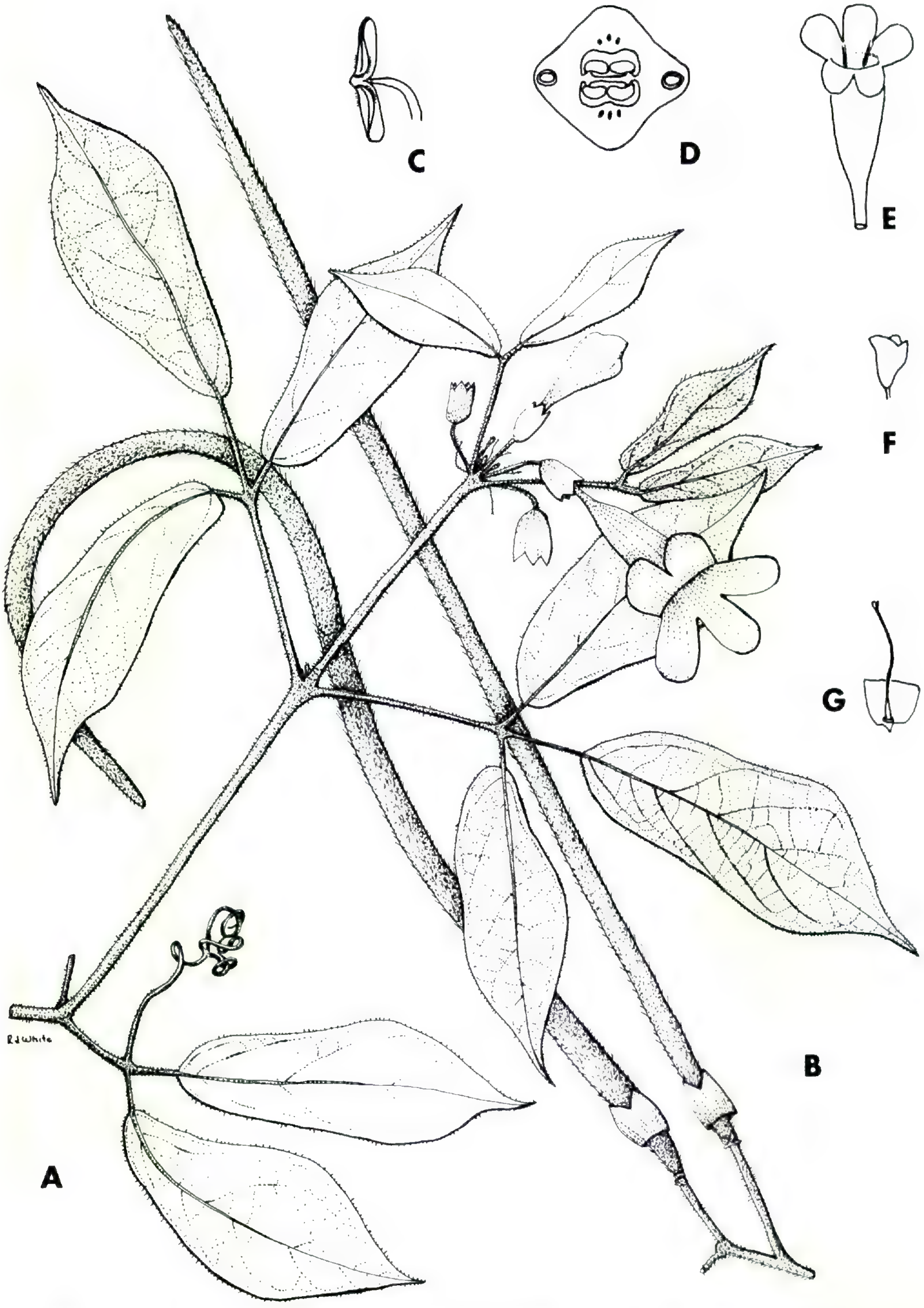


FIGURE 35. *Stizophyllum*.—A–B. S. *inaequilaterum* Bur. & K. Schum.—A. Habit (× ½). [After *Gentry 7383* (MO).]—B. Fruit (× ½). [After *Lewis et al. 5257* (MO).]—C–G. S. *riparium* (H.B.K.) Sandw.—C. Anther (× 3½).—D. Ovary cross section (× 15).—E. Corolla (× ½).—F. Calyx (× ½).—G. Pistil and disc (× ½). [After *Gentry 2075* (MO).]

simple, usually kinky trichomes, the nodes without interpetiolar glandular fields; pseudostipules usually inconspicuous or lacking, sometimes linear with a thickened tip. *Leaves* 3-foliolate or 2-foliolate with tendril or tendril scar; leaflets more or less oblong-elliptic, acuminate, asymmetrically truncate or subcordate, 5.6–13.1 cm long and 3.0–6.1 cm wide, membranaceous, sometimes inconspicuously serrulate, more or less pinnately veined to the base, secondary nerves 4–7 on a side, regularly sunken-lepidote glandular below, hence pellucid punctate, hirsute on nerves, especially beneath with long, simple trichomes, these arising sporadically from even minute reticulations, drying dark olive to yellowish-olive, the veins usually brownish beneath; tendril trifid, 8–16 cm long to branching, the 3 arms 0.6–2 cm long; terminal petiolules 1.1–3.7 cm long, lateral petiolules 0.4–2.3 cm long, petiole 2.2–7.5 cm long, pubescent with long simple curly trichomes. *Inflorescence* a long-bracteate, few-flowered terminal fascicle or a contracted raceme terminal on a young lateral shoot, the branches hirsutely reddish-pubescent, the bracts linear, pubescent, to 2 cm long. *Flowers* with the calyx membranaceous, inflated-campanulate, 12–18 mm long and 9–10 mm wide, the edge irregular, drying light green, slightly lepidote and sparsely hirsute, usually with glands; corolla greenish-yellow with lavender lobes, 5–6.5 cm long and 1–1.5 cm wide at the mouth, the tube 3.8–4.8 cm long, the lobes 0.8–1.0 cm long, the tube glandular-lepidote and puberulous outside, the lobes pubescent, the tube mostly glabrous inside; stamens didynamous, the anther thecae divaricate, sparsely ciliate with short trichomes along the margins, ca. 2 mm long, the longer filaments 2–2.1 cm long, shorter filaments 1.5–1.6 cm long, inserted 1.3–1.4 cm from the base of the tube; pistil and ovary not seen in the 2 flowers available for study. *Capsule* linear, narrow, subterete in cross section, 30–32.5 cm long and 4–5 mm wide, densely hirsute or villous.

A rarely collected vine of the tropical wet forest and premontane wet forest, it is sometimes locally common but inconspicuous both in flower and fruit. Flowering collections from Panama have been made in April and May.

This species is superficially similar to its congener, *S. riparium*, but field study has shown the two species are readily distinguished even when sterile. The coarser, more conspicuous, reddish-brown pubescence of twigs and leaves of this species contrasts markedly with the dense, short, whitish-appearing puberulence of *S. riparium*. *Stizophyllum inaequilaterum* lacks the conspicuous strap-shaped pseudostipules of young twigs of *S. riparium*, and the tendrils are trifid, while those of *S. riparium* are simple; also the calyx and fruit of this species are pubescent with much longer trichomes than those of *S. riparium*.

CANAL ZONE: Pipeline Road, *Gentry 706, 1234, 1452, 3163* (all MO). Cultivated at Summit Garden, *Gentry 7383* (MO). COLÓN: Santa Rita Ridge, *Gentry 466, 1882A* (both MO); *Lewis et al. 5257* (MO). Hillside above Portobelo, *Gentry 731C* (MO). DARIÉN: Base of Cerro Pavarandó, *Gentry 4212* (MO). PANAMÁ: E of Cañitas, *Gentry 3694* (MO). SAN BLAS: Mainland opposite Playón Chico, *Gentry 6363* (MO).

2. **Stizophyllum riparium** (H.B.K.) Sandw., Lilloa 3: 462. 1938.—FIG. 35C–G.

Bignonia riparia H.B.K., Nov. Gen. Sp. Pl. 3: 138. 1819. TYPE: Colombia, Río Magdalena, *Humboldt & Bonpland s.n.* (P).

B. brevipes Rusby, Bull. Torrey Bot. Club 27: 72. 1900. TYPE: Bolivia, Junction of Beni and Madre de Dios Rivers, *Rusby 1144* (NY).
Adenocalymma flos-ardeae Pittier, Contr. U. S. Natl. Herb. 18: 256. 1917. TYPE: Panama, Colón, *Pittier 3898* (BM, NY, US).
A. punctifolium Blake, Contr. U. S. Natl. Herb. 24: 22. 1922. TYPE: Guatemala, Izabál, *Pittier 8570* (GH, NY, US).
Stizophyllum flos-ardeae (Pittier) Sandw., Recueil Trav. Bot. Néerl. 34: 212. 1937.
S. punctifolium (Blake) Sandw., Recueil Trav. Bot. Néerl. 34: 212. 1937.

Liana to at least 5 cm in diameter, the bark smooth, vertically striate; stem subtetragonal with hollow center and 4 phloem arms in cross section; branchlets terete, hollow, longitudinally striate, densely short-puberulent, the nodes without interpetiolar glandular fields, often with lines connecting opposite petioles; pseudostipules strap-shaped, caducous. *Leaves* 3-foliolate or 2-foliolate with tendril or tendril scar; leaflets ovate or obovate to oblong-elliptic, acute to acuminate, truncate to subcordate, 2.9–20 cm long and 1.9–12.5 cm wide, membranaceous, often serrate when young, palmately nerved at the base, the secondary veins (3–)4–6 on a side, regularly sunken-lepidote beneath, hence pellucid-punctate at least when mature, puberulous on the nerves with short simple trichomes especially beneath, drying olive to brownish with the veins tannish beneath; tendril simple or rarely bifid with second arm minute, 7–15 cm long; terminal petiolules 3.2–7.2 cm long, lateral petiolules 0.7–4.0 cm long, petiole 2.0–11.0 cm long, short-puberulous. *Inflorescence* a few-flowered axillary raceme, the narrowly bracteate rachis and pedicels puberulous. *Flowers* with inconspicuous sweet odor, calyx infundibuliform, irregularly 5-lobed to bilabiate, 5–12 mm long and 4–10 mm wide, densely puberulous, glandular on the lobes; corolla uniformly white to cream, tubular, 3.2–5.0 cm long and 0.7–1.3 cm wide at the mouth, the tube 3.4–4.1 cm long, the lobes 0.5–0.8 cm long, puberulous outside with moniliform, glandular-lepidote, and simple trichomes, pubescent inside with moniliform trichomes on the lobes and with gland-tipped trichomes at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, sometimes slightly pubescent, 2–2.5 mm long, the longer filaments 1.5–1.8 cm long, shorter filaments 1.1–1.2 cm long, the staminode 3–5 mm long, inserted 10–12 mm from base of corolla tube; pistil 2.7–3.1 cm long, the ovary linear, tetragonal, 3.5–4 mm long and 1 mm wide, glandular-lepidote, the ovules 2-seriate in each locule; disc short-cupular, 1 mm long and 2.5–3 mm wide. *Capsule* linear, tapering toward the ends, not flattened, 24–45 cm long and 0.5–0.7 cm wide, the surface longitudinally finely striate, short-puberulous; calyx usually caducous; seeds 0.4–0.5 cm long and 1.3–2.4 cm wide, the wings membranaceous, brown, weakly demarcated.

One of the commonest vines of the tropical moist forest, this species also occurs sporadically in premontane wet forest and uncommonly in tropical wet forest. Despite the great abundance of sterile young plants, it is seldom encountered in flower or fruit and is poorly represented in herbaria. It ranges from Mexico to Peru and Bolivia. This species flowers mostly during the wet season from April to November.

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2686* (MO). CANAL ZONE: Barro Colorado Island, *Croat 10220* (MO, SCZ); *Gentry 5161* (MO); *Kenoyer 534* (US); *Shattuck*

12 (A, F, MO); *Standley 40923* (US); *Wetmore & Woodworth 40* (A); *Zetek s.n.* (F, pro parte). Along road to La Pita Signal Station, *Croat 13957A* (MO, SCZ). Fort Sherman, *Duke 4383* (K). Boy Scout road near Madden Lake, *Gentry 1375, 2052* (both MO). Las Cruces Trail in Madden Forest, *Gentry 1384* (MO). Pipeline Road, *Gentry 2075, 2468* (both MO); *Gentry & Dressler 1964* (MO). Barbacoas Station, Panama Railroad, *Hayes 736* (BM, K). Río Pedro Miguel near east Paraíso, *Standley 29936* (US). CHIRIQUÍ: 12 mi. N of Puerto Armuelles, *Croat 21975* (MO). Burica Peninsula along Quebrada Tuco, *Croat 22115* (MO). W of San Bartolo Limite near Costa Rican border, *Croat 22165* (MO). Along highway between Ríos Tinta and Tabasara, *Woodson et al. 386* (MO). COLÓN: Vicinity of Río Piedras along road to Portobelo, *Blum et al. 2505* (SCZ). Ridge W of Portobelo, *Gentry 1767* (MO). Along Río Fató, *Pittier 3898* (BM, NY, US). DARIÉN: Río Tuira between Río Punusa and Río Mangle, *Duke 14628*. S of Jaqué, *Gentry 4171* (MO). Santa Fé, *Gentry 4309* (MO). Village of Paya, *Gentry 4394* (MO). Between Ríos Cube and Punusa, *Gentry 4468* (MO). El Real, *Gentry 4510* (MO). Near Cerro Pirre on Río Parasenico, *Gentry 4689* (MO). PANAMÁ: Cañitas, *Gentry 1407* (MO). Trail along Río Pacora S from Pacora, *Gentry 1413* (MO). Dam site on Río Bayano, *Gentry & Tyson 1678* (MO). Río Pasiga, *Gentry 2196, 2265, 2278* (all MO). Río Maestro, *Gentry 2228* (MO). Río Piragua (Tabardí), *Gentry 2530* (MO). Icantí, *Gentry 2628* (MO). Near Capira, *Gentry 3152* (MO). Ca. 16 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3811* (MO). Near Río Espavé, *Gentry 3696* (MO). Near archeological site at edge of Madden Lake, *Gentry 5009* (MO). Between Pacora and Chepo, *Gentry 5115* (MO). Pacora, *Maurice 814* (MO, US). Juan Díaz, *Standley 30480* (US). SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1481* (MO). VERAGUAS: Santiago, *Dwyer 1345* (MO).

36. TABEUIA

Tabebuia Gomes *ex* DC., Rev. Bign. (Bibl. Univ. Genève) 14. 1838. TYPE: *T. uliginosa* (Gomes) DC. = *T. cassinoides* (Lam.) DC.

Couralia Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 14. 1842. TYPE: *C. fluviatilis* (Aubl.) Splitg. = *Tabebuia aquatilis* (E. Meyer) Sprague & Sandw.

Handroanthus Mattos, Loefgrenia 50: 1. 1970. TYPE: *H. albus* (Cham.) Mattos = *Tabebuia alba* (Cham.) Sandw.

Shrubs to giant *trees*. *Leaves* simple, 1-foliolate, or digitately 3–7-foliolate. *Inflorescence* terminal, an open or congested panicle or raceme, or reduced to a single flower. *Flowers* with the calyx cupular, campanulate or tubular, truncate, bilabiate or shallowly 5-lobed; corolla white, yellow, lavender, magenta, or red, tubular-infundibuliform to tubular-campanulate (Panama), glabrous or puberulous on the tube outside; anthers glabrous, the thecae straight, divaricate; pollen grains single, 3-colpate, the exine finely reticulate; ovary linear oblong, often somewhat lepidote, the ovules 2-multi-seriate in each locule. *Fruit* a subterete elongate-linear or short oblong capsule, dehiscing more or less perpendicularly to the septum, smooth to irregularly wavy-muricate, glabrous to lepidote or variously pubescent; seeds thin and bialate with hyaline-membranaceous wings, or thick, corky and suborbicular without wings

Fewer than 100 species in tropical America ranging from northern Mexico and the West Indies to northern Argentina.

Useful references:

Buchinger, M. Las especies Argentinas del género *Tabebuia*. Rev. Invest. Forest. 2: 3–30. 1960.

Dugand, A. Bignoniaceae: El género *Tabebuia* en Colombia. Mutisia 25: 1–31. 1956.

Gentry, A. H. A revision of *Tabebuia* (Bignoniaceae) in Central America. Brittonia 22: 246–264. 1970.

a. Leaflets not stellate-pubescent; flowers (where known) rose, purple, or white; calyx glandular-lepidote or mealy pubescent (if pubescent, corolla puberulous outside); fruit glandular-lepidote or glabrous, the surface smooth.
  b. Leaflets glandular-lepidote, not pubescent, linear-oblong to elliptic-oblong; corolla (where known) glabrous outside; calyx and fruit strongly glandular-lepidote.
    c. Leaves simple to 3-foliolate, blades linear-oblong; inflorescence (where known) few-flowered; corolla (where known) white.
      d. Tree; leaves simple; calyx (at least in fruit) spathaceously split and striate with 5 raised lines; fruit linear, more than 12 cm long; seeds thin, bialate; well-drained sites ..... 8. *T. striata*
      dd. Shrub or small tree; leaves simple to 3-foliolate; calyx 2–3-labiate, not striate; fruit oblong, less than 12 cm long, attenuate at both ends; seeds thick, corky, wingless; Pacific coast mangrove swamps ..... 6. *T. palustris*
    cc. Leaves mostly 5-foliolate, blades elliptic-ovate to elliptic-oblong; inflorescence few- to many-flowered; corolla pale pink, rose, or lavender, rarely white.
      e. Leaflets acuminate or sharply acute; inflorescence usually many-flowered; mature capsule more than 22 cm long; native and cultivated ..... 7. *T. rosea*
      ee. Leaflets obtuse; inflorescence few-flowered; mature capsule usually less than 15 cm long; rarely cultivated ..... 5. *T. pallida*
  bb. Leaflets pubescent at least in axils of lateral nerves beneath, ovate to ovate-lanceolate; corolla puberulous outside; calyx mealy pubescent; fruit glabrous ..... 3. *T. impetiginosa*
aa. Leaflets stellate-pubescent at least in axils of lateral nerves beneath; flowers yellow; corolla glabrous outside or with a few trichomes below sinuses; calyx with at least vestigial yellowish to reddish-stellate tomentum; fruit stellate to woolly pubescent, or if only inconspicuously lepidote then wavy-muricate.
  f. Leaflets pubescent only in axils of lateral nerves beneath; the leaves often 7-foliolate; calyx sparingly thick-stellate pubescent; fruit more or less lepidote, wavy-mucronate ..... 2. *T. guayacan*
  ff. Leaflets with stellate trichomes scattered over undersurface or along veins; the leaves rarely 7-foliolate; calyx stellate-pubescent, usually also with longer barbate or simple trichomes; fruit with some stellate trichomes.
    g. Leaves pubscent mostly along veins and petioles; corolla lobe venation of dried specimens conspicuously reticulate to the margins, the color of lobes same as that of tube; calyx without long simple trichomes, pubescent with short stellate trichomes sometimes with some barbate trichomes, its lobes reflexed; fruit more or less rugose, shortly stellate-pubescent; tropical wet forest (in Panama and Costa Rica) ..... 1. *T. chrysantha*
    gg. Leaves densely pubescent over whole surface beneath; corolla of dried specimens with venation becoming obscure in the lobes, the lobes appearing yellow and distinctly different from darker-drying corolla tube; calyx golden woolly-pubescent with many long (to 7 mm) simple trichomes in addition to the short-stellate tomentum, its lobes erect; fruit woolly-pubescent; mostly in tropical dry forest and drier parts of tropical moist forest ..... 4. *T. ochracea*

1. **Tabebuia chrysantha** (Jacq.) Nichols., Dict. Gard. 4: 1. 1887.

Bignonia chrysantha Jacq., Hort. Schoenb. 2: 45, *tab. 211*. 1797. TYPE: Venezuela, Caracas (not seen).
Tecoma chrysantha (Jacq.) DC., Prodr. 9: 221. 1845.
Tabebuia rufescens J. R. Johnston, Proc. Amer. Acad. Arts 40: 696. 1905. TYPE: Venezuela, Margarita Island, *Johnston 79* (GH).
Tecoma evenia Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 8. 1895, pro parte. TYPE: Guatemala, Santa Rosa, *Heyde & Lux 3110* (MO; US, flowers only).
Tabebuia glomerata Urb., Fedde Repert. 14: 305. 1916. SYNTYPES: Trinidad, Tobago, Jamaica (not seen).

Tecoma palmeri Kränzl., Fedde Repert. 17: 220. 1921. TYPE: Mexico, Guerrero, *Palmer 419* (K, MO, US).

Tree to 25 m tall and 50 cm d.b.h., the bark pale to dark gray, scaly; wood hard and heavy, dark olive brown with yellow (lapachol) deposits in the vessels; twigs subtetragonal, varyingly stellate-pubescent when young, glabrescent, the nodes without interpetiolar glands or pseudostipules. *Leaves* palmately 5(–7)-foliolate; the leaflets broadly elliptic to oblong-obovate, abruptly acuminate, obtuse to truncate or asymmetrically subcordate, the terminal leaflet 6–27 cm long and 4–12.3 cm wide, the intermediate leaflets 5–25 cm long and 3.4–11 cm wide, the lateral leaflets 2.5–14 cm long and 1.4–8.3 cm wide, entire or serrate, membranaceous to rigid-chartaceous, lepidote above and beneath, sometimes stellate-pubescent above, always to some extent beneath especially along main veins, the trichomes scattered over the lamina; terminal petiolule 1.2–9 cm long, intermediate petiolules 0.7–6.7 cm long, lateral petiolules 0.3–2.1 cm long, the petiole 5–23 cm long, stellate-pubescent to glabrate. *Inflorescence* a contracted terminal panicle, the branches stellate-pubescent, the bracts extremely reduced. *Flowers* slightly aromatic, calyx campanulate, 5-lobed, the lobes often more or less reflexed, 5–13 mm long and 4–12 mm wide, shortly stellate-pubescent; corolla tubular-infundibuliform, 3–8 cm long, yellow with reddish penciling in the throat and the venation (dried) reticulate to the margins of the lobes, the dried tube and lobes indistinguishable in color, the tube 2.2–5 cm long and 0.6–2.2 cm wide at the mouth, the lobes 0.9–2.6 cm long, glabrous outside and 4 lines of simple or usually once-branched, 2–3-celled trichomes extending inside from the 4 lower sinuses to the level of stamen insertion, the level of stamen insertion glandular-pubescent; stamens didynamous, inserted 4–8 mm from the base of the corolla tube, the longer filaments 1.6–2.2 cm long, shorter filaments 1.0–1.5 cm long, the anther thecae divaricate, 2–3 mm long, the staminode 4–9 mm long; pistil 1.8–3.1 cm long, the ovary linear, 3.5–5 mm long and 1.5–2 mm wide, glabrous to lepidote or sparsely stellate-pubescent, the ovules 8–10-seriate in each locule; disc pulvinate, 0.5–1 mm long and 2–3 mm wide. *Capsule* linear-cylindric, tapered at the ends, to 50 cm long and 2.0 cm wide, sparingly short stellate pubescent; seeds 0.4–0.9 cm long and 1.4–3.3 cm wide, the wings hyaline-membranaceous, well demarcated from the seed body.

A perplexing species, *Tabebuia chrysantha* includes at least two ecologically distinct but morphologically similar forms. As now understood, one of these occurs from Mexico to Honduras and in Trinidad and northern Venezuela mostly in tropical dry forest. The other ranges from Nicaragua to Venezuela in tropical and premontane wet forest.

This species flowers during the dry season with collections of flowers made mostly in February and March. A single August collection (*Gentry* 5681) with flowers was made during the abnormally dry wet season of 1972.

Despite an extensive search I was unable to locate type material of Jacquin's *Bignonia chrysantha*. The illustration in *Hortus Schoenbrunnensis* matches either the plant of the Venezuelan dry forest which has been known as *T. rufescens* or the otherwise unnamed wet forest entity which I also include under *T. chry-*

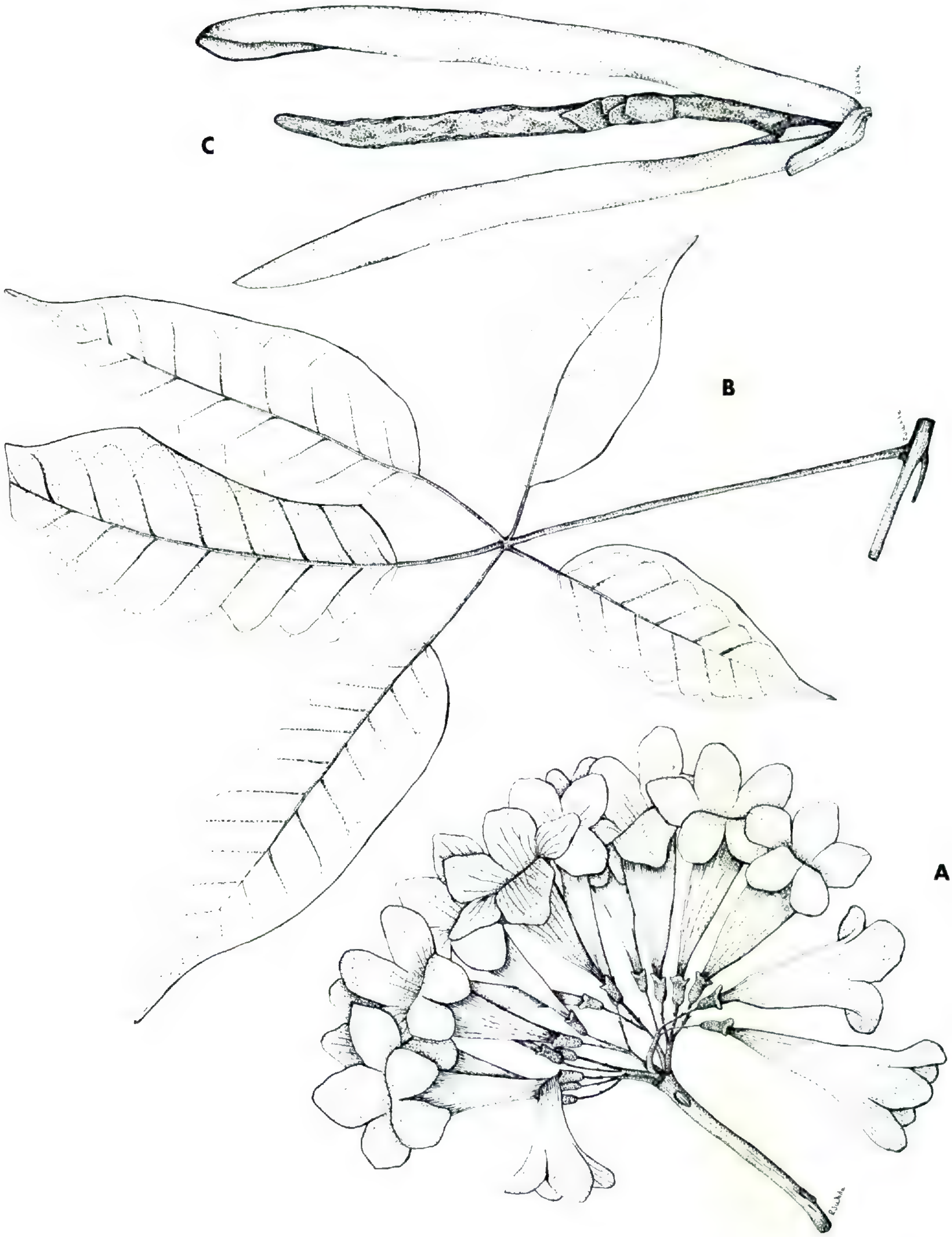


FIGURE 36. *Tabebuia*.—A–B. *T. guayacan* (Seem.) Hemsl.—A. Inflorescence (× 2/5). [After *Croat* 5388 (MO).]—B. Leaf (× 2/5). [After *Gentry* 4287 (MO).]—C. *T. striata* A. Gentry, fruit (× 2/5). [After *Gentry* 1404 (MO).]

santha. *Tabebuia chrysantha* of Venezuela and Trinidad is almost identical with the *T. chrysantha* of Mexico and northern Central America, but in the intervening area of Costa Rica and Panama only the wet forest form of the species occurs.

CANAL ZONE: Pipeline Road, *Gentry 1795* (MO, SCZ), *2461* (MO). CHIRIQUÍ: Burica Peninsula along Quebrada Guanabano, *Croat 22514* (MO). Puerto Armuelles, *Liesner 136* (MO). Area W of Puerto Armuelles, *Stern & Chambers 130* (NY, US). COCLÉ: Base of Cerro Pilón, *Gentry & Dwyer 3661* (MO). Above El Valle, *Gentry 5681* (MO). COLÓN: Santa Rita Ridge, *Gentry 456* (MO, WIS). DARIÉN: Base of Cerro Pavarandó, *Gentry 4211* (MO). Base of Cerro Pirre, *Gentry 4584* (MO). Summit of Cerro Pirre, *Gentry 4611* (MO). PANAMÁ: W of El Llano, *Gentry 5074* (MO). VERAGUAS: Mountains above Santa Fé, *Gentry 3082* (MO).

2. **Tabebuia guayacan** (Seem.) Hemsl., Biol. Centr. Amer. Bot. 2: 495. 1882. —FIG. 36A–B.

Tecoma guayacan Seem., Bot. Voy. Herald 180. 1854. TYPE: Panama, Cruces, *Seemann 398* (BM, K).

Tree to 50 m tall and 2 m d.b.h., the bark split by long, shallow, vertical furrows with the plates between furrows broken into scales, light tan or buff to gray brown in color; wood extremely hard, the heavy heartwood dark olive brown with yellow (lapachol) deposits in the vessels; twigs subtetragonal, glabrous, the nodes without interpetiolar glands or pseudostipules. *Leaves* palmately 5–7-foliolate; the leaflets lanceolate to ovate, acuminate, basally rounded to obtuse, the terminal leaflet 9–30 cm long and 3.7–15.5 cm wide, the intermediate leaflets 8–30 cm long and 2.8–15 cm wide, the lateral leaflets 6–21.5 cm long and 2.1–10.7 cm wide, these often partially divided (if complete leaflets 7, the basal pair smaller), entire (or serrulate in seedlings), membranaceous, minutely lepidote at least beneath, stellate-pubescent with multicellular usually 3-branched trichomes in the axils of lateral nerves beneath; terminal petiolule 2.9–7.4 cm long, intermediate petiolule 2.4–6.0 cm long, lateral petiolule 1.1–3.4 cm long; petiole 7–23 cm long, glabrous. *Inflorescence* a terminal panicle, the flowers in 2's or 3's, the branches slightly stellate-rufescent with reduced, caducous bracts. *Flowers* with very faint odor, calyx campanulate, irregularly 2–5-lobed, 7–15 mm long and 2–12 mm wide, sparsely stellate pubescent with short thick trichomes; corolla yellow with reddish penciling in the throat; tubular-infundibuliform, 6–11 cm long and 1.3–2.2 cm wide at the mouth of tube, the tube 3.6–5.7 cm long, the lobes 2.2–3.8 cm long, glabrous outside, inside with long mostly branched, 3–4-celled trichomes in the sinuses and from the 4 lower sinuses to the level of stamen insertion, glandular-pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2–3 mm long, the longer filaments 15–21 mm long, shorter filaments 11–16 mm long, the staminode 3–10 mm long, inserted 4.5–8 mm from the base of the corolla tube; pistil 2.4–3.3 cm long, the ovary linear, 3–5 mm long and 1.5–2.5 mm wide, glabrous to somewhat lepidote, the ovules 9–10-seriate in each locule; disc cupular, 0.5–1 mm long and 3–4 mm wide. *Capsule* linear-cylindric, 29–61 cm long and 1.0–2.9 cm wide, essentially glabrous or inconspicuously lepidote or thick-stellate pubescent; seeds 0.9–1.1

cm long and 3.5–4.0 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A tree of the tropical moist forest, *Tabebuia guayacan* occurs also, but sparingly, in the premontane wet forest. It ranges from southern Mexico to Colombia. This species flowers almost entirely during the dry season from January to May with an occasional individual blooming asynchronously during the wet season. Seed release occurs during the late dry season and early wet season; the seeds are wind-dispersed.

Tabebuia guayacan can be recognized vegetatively by the stellate trichomes beneath in the axils of the lateral nerves of an otherwise glabrous leaflet and by its tendency to 7-foliolate leaves. It is closely related to *T. serratifolia* (Vahl) Nichols., a species widespread in South America, which differs in its simple trichomes in the axils of the lateral nerves beneath and in the longer trichomes inside the corolla tube.

CANAL ZONE: Barro Colorado Island, *Carpenter 66* (F); *Croat 4120* (SCZ), *4121*, *5388*, *7940* (all MO, SCZ); *Gentry 450* (MO, WIS), *712A* (MO); *Shattuck 821* (F, MO); *Standley 31419* (US). Near Gamboa, *Allen 228* (A, GH, US). Río Cristal on Pan Am Highway, Playa Coronado, *Croat 14256* (MO). Balboa, *Gentry 423* (MO, WIS). Pipeline Road, *Gentry 1586*, *2410*, *4788* (all MO). Road to Gamboa airport, *Gentry 2045*, *4855* (both MO). Albrook NCO Club, *Gentry 1736* (MO). Road K-10 at edge of Canal Zone, *Gentry 1958* (MO). Vicinity of Summit Garden, *Gentry 4284*, *5119* (both MO). Around Gamboa, *Pittier 2694* (BM, GH, NY, US). Near village of Cruces, *Seemann 398* (BM, K). Summit, *Sharp s.n.* (SCZ). Hills N of Frijoles, *Standley 27532* (US). Albrook NCO Club, *Tyson 5403* (MO, SCZ). N of Summit, *Woodson et al. 768* (A, MO, NY, US); *Woodworth & Vestal 732* (F). Without locality, *Johansen 72* (US). CHIRIQUÍ: Progreso, *Cooper & Slater 311* (F, US). COLÓN: Along Río Boqueron above Peluca Hydrographic Station, *Hunter & Allen 656* (G, GH, MO, NY). DARIÉN: Vicinity of Pinogana, *Allen 4294* (GH, MO). S of La Palma, *Gentry 4287* (MO). Near village of Pirre, *Gentry 4781* (MO). PANAMÁ: Ciudad de Panamá, *Gentry 1940* (MO, SCZ); *Holdridge 6477* (PMA).

3. **Tabebuia impetiginosa** (Mart. *ex* DC.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 176. 1936.

Bignonia heptaphylla sensu auct., non Vell. Fl. Flum. 6: 251. 1825; *pl. 48*. 1827.
Tecoma heptaphylla (Vell.) Mart., Flora 24, Beibl. 2: 13. 1841, sensu auct. non Vell.
Tecoma impetiginosa Mart., Syst. Mat. Med. Veg. Bras. 54. 1843, nomen nudum.
T. ipe Mart., Syst. Mat. Med. Veg. Bras. 55. 1843, nomen nudum.
T. impetiginosa Mart. *ex* DC., Prodr. 9: 218. 1845. TYPE: Brazil, Piauhy, *Martius 2446* (G-DC, M).
T. eximia Miq., Linnaea 22: 803. 1849. LECTOTYPE: Brazil, Bahia, *Blanchet 3963*, leaves, flowers excluded (BR, C, G, K, MO, P, U).
Tabebuia avellanedae Lorentz *ex* Griseb., Symb. Fl. Argent. 258. 1879. TYPE: Argentina (not seen).
T. palmeri Rose, Contr. U. S. Natl. Herb. 1: 109. 1891. TYPE: Mexico, Sonora, *Palmer 320* (GH, US).
Tecoma impetiginosa var. *lepidota* Bur., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 114. 1894. TYPE: Brazil, Rio de Janeiro, *Glaziou 11241* (P).
T. ipe Mart. *ex* K. Schum. *in* Engler & Prantl, Nat. Pflanzenf. 4(3b): 238. 1894. TYPE: Brazil (not seen).
T. adenophylla K. Schum. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 412. 1897. TYPE: Brazil, Goyaz, *Glaziou 21841* (BR, C).
Gelseminum avellanedae (Lorentz *ex* Griseb.) Kuntze, Rev. Gen. Pl. 3, 2: 245. 1898.
Tecoma ipe var. *integra* Sprague, Bull. Herb. Boiss., sér. 2. 5: 86. 1905. TYPE: Paraguay, *Hassler 3065* (K).

Tecoma avellanedae (Lorentz *ex* Griseb.) Speg. *in* Speg. & Girola, Cat. Descr. Maderas 379. 1910.
T. avellanedae var. *alba* Lillo, Segunda Contr. Conoc. Arbol. Argen. 13. 1917. TYPE: Argentina (not seen).
T. integra (Sprague) Chodat, Bull. Soc. Bot. Genève, sér. 2. 9: 242. 1917.
Tabebuia nicaraguensis Blake, Contr. Gray Herb. 52: 95. 1917. TYPE: Nicaragua, Hacienda Campuscus, *Baker 2258* (GH, holotype; MO, US, isotypes).
T. dugandii Standl., Trop. Woods 36: 17. 1933. TYPE: Colombia, Atlantico, *Dugand 345* (F, US).
T. ipe (Mart. *ex* Schum.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 176. 1936.
T. eximia (Miq.) Sandw., Lloydia 2: 213. 1939.
T. avellanedae var. *paulensis* Toledo, Arquiv. Bot. Est. São Paulo, n. s. 3: 33. 1952. TYPE: Brazil (not seen).
T. heptaphylla (Vell.) Toledo, Arquiv. Bot. Estado São Paulo, n. s. 3: 33. 1952, sensu auct. non Vell.
T. schunkevigoi Simpson, Fieldiana, Bot. 36: 1. 1972. TYPE: Peru, Huanuco, *Schunke 2596* (F, holotype; MO, isotype).

Tree to 20 m tall and 70 cm d.b.h., the bark relatively smooth, gray; wood greenish brown, dense, the vessels containing yellow powder (lapachol); twigs terete, glabrate, tips of shoots mealy pubescent, the nodes without interpetiolar glands or pseudostipules. *Leaves* palmately 5–7-foliolate, often anisophyllous; the leaflets ovate to elliptic, acuminate, cuneate to rounded or almost subcordate, the terminal leaflet 5–19 cm long and 1.5–8 cm wide, the intermediate leaflet 4–16 cm long and 2.8–9 cm wide, the basal leaflet 2.2–11 cm long and 1.5–8.3 cm wide, entire or serrulate, membranaceous to chartaceous, somewhat lepidote above and beneath, pubescent with simple or forked trichomes at least in the axils of lateral veins beneath or pubescent over the whole undersurface, often puberulous on the midrib above; terminal petiolules 1–4.2 cm long, intermediate petiolules 0.9–4 cm long, lateral petiolules 0.2–2 cm long, the petiole 4–13 cm long, lepidote and puberulous. *Inflorescence* a terminal, usually more or less congested panicle, the flowers in 3's, the branches whitish to tannish mealy-pubescent with short, thick-stellate trichomes. *Flowers* with the corolla pinkish-purple to deep magenta outside and on the lobes, the throat opening yellow, turning magenta, tubular-campanulate, 4–7.5 cm long and 1.2–5 cm wide at the mouth, the tube 2.5–5 cm long, the lobes 0.9–2.0 cm long, puberulous outside, inside with a few, scattered, simple trichomes in the tube and pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2.5–3.5 mm long, the longer filaments 1.6–2.3 cm long, shorter filaments 1.0–1.6 cm long, the staminode 3–7 mm long, inserted 5–6 mm from the base of the corolla tube; pistil 2.7–3.4 cm long, the ovary linear, 3–4 mm long and 1 mm wide, subtetragonal in cross section, glabrous to slightly lepidote, the ovules ca. 4-seriate in each locule; disc cupuliform, 1–1.5 mm long and 2 mm wide. *Capsule* elongate-cylindrical, attenuate at both ends, 12–56 cm long and 1.3–2.5 cm wide, glabrous; seeds 1–1.6 cm long and 3–4.8 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A characteristic tree of the premontane moist forest, *Tabebuia impetiginosa* also occurs to some extent in the tropical dry forest. It ranges from northern Mexico to Argentina. This species flowers in the early dry season from December to February. The wind-dispersed seeds are released in late dry season.

The name *Tabebuia impetiginosa* has been used only in central Brazil where it has been separated from the other species of a wide ranging complex because of its pubescent leaflets. However, pubescent-leaved plants occur as occasional variants throughout the range of the species in Central America, and have been named as *T. nicaraguensis*. In Brazil the glabrate form has been given the names *T. impetiginosa* var. *lepidota* and *T. adenophylla*.

Geographical separation and characters of the number of leaflets and leaf indumentum have been used to maintain these various populations as separate species. Disjunctions in the range of this composite species are like those of a number of other organisms which are restricted to the dry forest habitat with the species occupying all of the suitable habitats, and the various populations separated only by the present expansion of the intervening wet forest areas.

The Central American, Colombian, and western Argentinian populations have 5-foliolate leaves with entire leaflets which are pubescent only in the axils of the lateral nerves below; the eastern Argentinian plants have mostly 7-foliolate leaves with dentate leaflets which are pubescent only in the axils of the lateral nerves beneath; and most Brazilian plants have entire leaflets which are pubescent over the whole lower surface.

Recent collections from the dry forest area around the Golfo de San Miguel, Darién Province, come from the middle of the supposed area of disjunction between the Central American and Colombian populations, further supporting the morphological evidence for union of *T. palmeri* and *T. dugandii* under *T. impetiginosa*. The Darién specimens are noteworthy in having the mostly 7-foliolate leaves of the Argentinian and some Brazilian forms.

The serrate-leaved form of eastern Argentina and adjacent Brazil was considered distinct by Buchinger (1960) as *T. ipe* (Mart. *ex* K. Schum.) Standl., but I suspect it merits varietal rather than specific recognition.

Most specimens identified as *Tabebuia heptaphylla* (Vell.) Toldeo belong to this species, and that name has been used (as *Tecoma heptaphylla*) in Brazil. The basionym *Bignonia heptaphylla* Vell. antedates the basionym of *Tabebuia impetiginosa*. Vellozo's drawing of a 7-foliolate, serrate-leafleted plant could refer to this species or several others. The description of the corolla as "violacea" points toward this species, but the strongly 5-dentate calyx does not. The fruit as figured and described is wrinkled-striate with a persistent calyx, conditions which do not match *T. impetiginosa*. In the absence of a type specimen, *B. heptaphylla* has been subject to diverse interpretations, and because of these several problems, I consider *Tabebuia heptaphylla* to be a *nomen confusum* and have adopted the name *T. impetiginosa*.

DARIÉN: Isla Cartagena, Golfo de San Miguel, *Gentry 3935* (MO). Shore near Majagualito across from La Palma, *Gentry 3989* (MO). Isla Encanto in Golfo de San Miguel, *Gentry 4023* (MO). PANAMÁ: Vicinity of Bejuco, *Allen 1630* (F, GH, NY, US), *4203* (MO).

4. **Tabebuia ochracea** (Cham.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 176. 1936.

Tecoma ochracea Cham., Linnaea 7: 653. 1832. TYPE: Brazil, *Sellow s.n.* (K, W).

T. hypodictyon DC., Prodr. 9: 217. 1845. TYPE: Brazil, Villa Barra, *Blanchet*, 1840 (G-DC).
T. hassleri Spr., Trans. Proc. Bot. Soc. Edinburgh 48: 435. 1904. SYNTYPES: Paraguay, San Estanislao, *Hassler 4159* (GH, K), *4164* (K).
Tabebuia hypodictyon (DC.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 176. 1936.

4a. **Tabebuia ochracea** subsp. **neochrysantha** (A. Gentry) A. Gentry, comb. & stat. nov.

T. neochrysantha A. Gentry, Brittonia 22: 260. 1970. TYPE: Costa Rica, Guanacaste, *Gentry* 355 (BM, F, MO, UC, US, WIS).
?*Bignonia heterotricha* DC., Rev. Bign. (Bibl. Univ. Genève) 22. 1838, nomen nudum.
?*Tecoma heterotricha* DC., Prodr. 9: 219. 1845. TYPE: Venezuela, Caracas, *Vargas s.n.* (G-DC).
?*Tabebuia heterotricha* (DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 495. 1882.
T. chrysantha (Jacq.) Nichols., Dict. Gard. 4: 1. 1897, sensu Sandw., non Jacq.

Tree to 25 m tall and 50 cm d.b.h., the bark with dark shallow vertical furrows separating lighter, flat-surfaced ridges; wood hard, heavy, the heartwood dark olive brown with yellow (lapachol) deposits in the vessels; twigs subtetragonal, stellate-pubescent when young, glabrescent, the nodes without glands or pseudostipules. *Leaves* palmately 5-foliolate; the leaflets oblong-obovate or oblong-elliptic, abruptly acuminate to apiculate, basally obtuse to truncate, the terminal leaflet 5–22 cm long and 1.8–14.4 cm wide, the intermediate leaflets 4.2–19.8 cm long and 1.4–13.2 cm wide, the lateral leaflets 2.8–11 cm long and 1.6–8.0 cm wide, entire to serrate, membranaceous, lepidote above and beneath, stellate pubescent but glabrescent above, densely and persistently stellate-pubescent beneath; terminal petiolule 0.8–5.8 cm long, intermediate petiolules 0.7–5.1 cm long, lateral petiolules 0.2–1.8 cm long, the petiole 6–18 cm long, stellate-pubescent. *Inflorescence* a contracted terminal panicle, the pedicels and peduncle obsolete, the branches stellate-pubescent. *Flowers* with a sweet fragrance, calyx campanulate, 5-lobed, 8–15 mm long and 5–1.0 mm wide, woolly-pubescent with shorter, stellate tomentum and thick covering of long (to 7 mm), simple trichomes, these usually branched at the extreme base; corolla yellow with reddish penciling in the throat, the venation drying obscure in the lobes, the tube and corolla different in color, the tube usually brownish, the lobes yellowish; tubular-infundibuliform, 4–8.3 cm long and 0.8–2.1 cm wide at the mouth, the tube 3–5.8 cm long, the lobes 1.0–2.4 cm long, glabrous outside except for some trichomes at the base of the lobes, villous on the anterior surface within, also with a few scattered simple trichomes adaxially in the throat, glandular-pubescent at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 1.5–2.5 mm long, the longer filaments 1.5–2.0 cm long, shorter filaments 0.9–1.5 cm long, the staminode 2–11 mm long, inserted 6–7 mm from the base of the corolla tube; pistil 2.0–2.7 cm long, the ovary linear, 3–5 mm long and 1.5–2 mm wide, lepidote to somewhat puberulous with simple and stellate trichomes, the ovules more or less 10-seriate in each locule; disc pulvinate, 1 mm long and 2–3 mm wide. *Capsule* linear-cylindric, tapered at the ends, 13–35 cm long and 1–1.5 cm wide, abundantly golden woolly pubescent with a short stellate tomentum and longer indumentum of simple trichomes (these usually with stellate base); seeds

0.4–0.8 cm long and 1.8–2.9 cm wide, the wings hyaline-membranaceous, well demarcated from the seed body.

A tree of the tropical dry forest, premontane moist forest, and drier parts of the tropical moist forest, *Tabebuia ochracea* subsp. *neochrysantha* occurs from Honduras and extreme eastern El Salvador to Venezuela and Trinidad. Other forms of the species occur south to Paraguay and Brazil. This species flowers in the dry season from January to April. The wind-dispersed seeds are released in mid to late dry season.

In the author's 1970 study the Central American population was considered to be distinct from related populations in South America, mainly on the basis of comparison of Central American material with the relevant types by curators of European herbaria. However, consultation of type material indicates that the Central American *T. neochrysantha* is conspecific with *T. ochracea* Cham., an earlier name.

There are overlapping quantitative differences between *T. neochrysantha* and *T. ochracea* which are geographically correlated. The northern form has usually longer calyx trichomes, a usually more conspicuous differentiation between corolla lobes and tube in dried specimens, somewhat shorter trichomes in the corolla tube, and an often softer leaf indumentum with usually less pronounced reticulation beneath. Sandwith in unpublished notes at Kew (K) separated this form as *T. chrysantha* from *T. ochracea* on the basis of its longer trichomes within the corolla tube on the anterior side, but this character shows too much variability for specific segregation. The evidence supports formal recognition for the northern plant, subspecies *neochrysantha*.

While the Brazilian type specimen of *Tecoma ochracea* (*Sellow s.n.*, duplicates at K, G-DC, W) is a reasonable match for Central American material of *T. neochrysantha*, I have as yet been unable to separate the South American taxa of this complex, some very different from Central American material, but it is probable that the Brazilian material will prove divisible into several species. However, the longer calyx trichomes and densely stellate-pubescent leaves, the most conspicuous characters of *T. neochrysantha*, are much more variable than previously supposed. Most Costa Rican populations have shorter calyx trichomes than those from Panama or Honduras, while juvenile leaves are normally much less thickly stellate pubescent than mature leaves of the same plant. *Tabebuia heterotricha*, although considered distinct in previous studies, is apparently an atypical form of this subspecies with less pubescent leaves similar to the common juvenile form.

CANAL ZONE: Ancon Hill, *Allen 4520* (G, MO). Balboa, *Gentry 424*. Madden Lake near Natural Bridge, *Gentry 701* (MO). Junction of Chiva Chiva Trail and Gaillard Highway, *Gentry 4786, 4861A, 4861B, 5117* (all MO). N of Paraiso, *Gentry 4958, 4959* (both MO). Ancón, *Keenan 323* (US). Sabanas, *Paul 307* (US). COCLÉ: S of El Valle de Antón, *Allen 4477* (G, MO). Penonomé and vicinity, *Williams 194* (NY). DARIÉN: Punto Sabanas opposite La Palma, *Gentry 3944* (MO). Punta Patiño NNE of Garachiné, *Gentry 4043* (MO). HERRERA: E of Las Minas, *Gentry 3146* (MO). PANAMÁ: Vicinity of Chorrera, *Allen 1698* (F, MO, NY, US), *4265* (G, GH, MO). Río Pasiga, *Gentry 2248* (MO). Farfan Beach road, *Gentry & Dwyer 3543* (MO). W of Cañitas, *Gentry 4964* (MO). Alhajuela, *Pittier 3501* (GH, NY, US). VERAGUAS: S of Santa Fé, *Gentry 2937* (MO). Near Río Santa María S of San Francisco, *Gentry 3118* (MO). WITHOUT LOCALITY: *Warscewicz 52* (G).

5. **Tabebuia pallida** (Lindl.) Miers, Proc. Roy. Hort. Soc. 3: 199. 1863.[8]

Bignonia pallida Lindl., Bot. Reg. 12: *tab. 965*. 1826. TYPE: St. Vincent, cultivated, *Caley s.n.* (not seen).

Shrub or small *tree*. *Leaves* 1–5-foliolate (in Panama mostly 5-foliolate) the leaflets elliptic to elliptic-oblong, obtuse, basally rounded, chartaceous, lepidote. *Inflorescence* a few-flowered terminal panicle, often reduced to one or 2 flowers. *Flowers* with the calyx cupular, bilabiate, lepidote; corolla pinkish-lavender to almost white, the throat opening yellow; tubular-infundibuliform; stamens didynamous, the thecae divaricate; ovary lepidote, the ovules 2-seriate in each locule. *Capsule* linear-cylindric, attenuate at both ends, 7–15 cm long (rarely to 22 cm, fide Sandwith, 1954), lepidote, the calyx persistent; seeds bialate, 7–9 mm long and 2–3 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A common and highly variable West Indian species, *T. pallida* is cultivated as an ornamental in various parts of the tropics. It is known in Panama only from a single tree at Summit Gardens. *Tabebuia pallida* is close to *T. rosea* but is separated by its usually smaller, obtuse leaflets.

CANAL ZONE: Summit Gardens, cultivated, *Nee & Mori 3579* (MO, WIS).

6. **Tabebuia palustris** Hemsl., Biol. Centr. Amer. Bot. 2: 495. 1882. TYPE: Panama, Canal Zone, *Hayes 80* (BM, K).

Shrub or small *tree*, often twisted, to 4 m tall and 5 cm d.b.h., the bark smooth, pale gray; wood whitish, soft; twigs terete, lepidote, the nodes without interpetiolar glandular fields or pseudostipules. *Leaves* simple or 3-foliolate; the leaflets narrowly elliptic or oblong, acute, cuneate to subsessile, the terminal leaflet 10–19 cm long and 2.1–5.6 cm wide, lateral leaflets when present 5–19 cm long and 1.1–5.1 cm wide, subcoriaceous, densely lepidote beneath, less so above, gray-green when dry, the terminal petiolule 1–3.5 cm long, lateral petiolules when present 0.2–1.5 cm long, the petiole 2.3–10 cm long, lepidote. *Inflorescence* a 2–5-flowered terminal cyme on a reduced branch usually in a dichotomy of the branches, the pedicels and peduncle lepidote. *Flowers* with the calyx irregularly bilabiate or 3-labiate, cupular, 10–20 mm long and 4–10 mm wide, lepidote; corolla white with yellow throat ridges, tubular-infundibuliform, 5–7 cm long and 0.9–1.5 cm wide at the mouth, the tube 2.8–5.8 cm long, the lobes 0.8–1.8 cm long, glabrous outside, inside pubescent on throat ridges and at the level of stamen insertion, sparsely so on lobes and in sinuses; stamens didynamous, the anther thecae divaricate, 3 mm long, the longer filaments 1.8–2.6 cm, shorter filaments 1.4–1.9 cm long, the staminode 5–7 mm long, inserted 4–6 mm from base of corolla, pistil 2.9–3.1 cm long, the ovary linear-conical, 4.5–5 mm long and 1 mm wide, densely glandular-

[8] The synonymy of this species is much more complex than indicated here, with many local varieties given specific epithets on different West Indian islands. Only these names have been used for Panamanian material.

lepidote, the trichomes extending up the base of style, the ovules 2-seriate in each locule; disc pulvinate, 2 mm long and 3 mm wide. *Capsule* oblong-cylindric, attenuate at both ends, 8–11 cm long and 1.6–2.6 cm wide, densely lepidote, the calyx persistent; seeds suborbicular, thick, corky, brown, 1.4–1.8 cm long and 1.8–2.2 cm wide, wings essentially lacking.

Restricted to coastal mangrove swamps and especially common along the mouths of rivers near the fresh water/salt water interchange, this seldom-collected plant ranges along the Pacific coast from central Costa Rica to Colombia. It blooms more or less throughout the year.

This species is distinct from other Central American species of Bignoniaceae in its shrubby habit, mangrove habitat and thick, corky seeds. Its closest relative is probably *T. aquatilis* (E. Meyer) Sprague & Sandw. of the Amazon and Orinoco valleys, which has similar fruit and seeds but 5-foliolate leaves with the veins drying reddish-yellow beneath. *Tabebuia insignis* of South America is also related but has winged seeds.

CANAL ZONE: Along creek at Miraflores Lock, *Gentry 422* (MO, WIS), *2104* (MO). Río Grande swamp, *Hayes 80* (BM, K). Miraflores Locks area, *Tyson 1269* (SCZ). Río Grande, *Woodson et al. 760* (A, MICH, MO, NY, US). COCLÉ: Penonomé and vicinity, *Williams 292* (NY, US). DARIÉN: Chepigana, *Duke & Bristan 282* (MO). 0–4 mi. up Río Sabanas from Santa Fé, *Duke 4148, 4172* (both MO). Río Sabanas just below Santa Fé, *Gentry 4080* (MO). Río Sabanas at junction with Río Lara, *Gentry 4084* (MO). Río Jaqué near mouth, *Gentry 4191* (MO). E of Santa Fé, *Tyson et al. 4679* (MO, SCZ). PANAMÁ: San José Island, *Erlanson 224, 330* (both GH, US); *Harlow 59* (GH); *Johnston 2* (GH, US), *798* (GH).

7. **Tabebuia rosea** (Bertol.) DC., Prodr. 9: 215. 1845.

Tecoma rosea Bertol., Fl. Guatimal. 25. 1840. TYPE: Guatemala, Esquintla, *Velasquez s.n.* (FI, fide Sandw.).
T. mexicana Mart. *ex* DC., Prodr. 9: 218. 1845. TYPE: Mexico, *Karwinski s.n.* (M).
Sparattosperma rosea (Bertol.) Miers, Proc. Roy. Hort. Soc. 3: 99. 1863.
Tabebuia mexicana (Mart. *ex* DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 495. 1882.
T. pentaphylla (L.) Hemsl., Biol. Centr. Amer. Bot. 2: 495. 1882, non *B. pentaphylla* L.
Couralia rosea (Bertol.) Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 9. 1895.
Tecoma evenia Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 9. 1895. TYPE: Guatemala, Santa Rosa, *Heyde & Lux 3110* (MO, US, leaves only).
T. punctatissima Kränzl., Fedde Repert. 17: 221. 1921. TYPE: Colombia, Cundinamarca, *Karsten s.n.* (W).
Tabebuia punctatissima (Kränzl.) Standl., Trop. Woods 36: 18. 1933.

Tree to 25 or 30 m tall and 1 m d.b.h., the bark narrowly vertically fissured with corky ridges, dark gray to blackish; wood superficially similar to oak, of medium density, light grayish brown with distinct pattern from stripings of brown paratracheal parenchyma, when fresh with faint sweet odor suggesting watermelon; twigs subtetragonal, lepidote, with thick pith, the nodes without interpetiolar glands or pseudostipules. *Leaves* palmately 5-foliolate, often anisophyllous; the leaflets elliptic to elliptic-oblong, acute to acuminate, basally rounded to cuneate, the terminal leaflet 8–35 cm long and 3–18 cm wide, the intermediate pair 6–34 cm long and 3–17 cm wide, the lateral pair 3.5–25 cm long and 1.4–12 cm wide, entire, subcoriaceous to chartaceous, lepidote above and beneath, gray-green when dry; the terminal petiolule 2–11 cm long, inter-

mediate petiolules 1.5–9.5 cm long, lateral petiolules 0.2–2.4 cm long, the petiole 5–32 cm long, lepidote. *Inflorescence* a terminal panicle with a pair of subulate bracts subtending each dichotomy, the branches densely lepidote. *Flowers* slightly sweet-smelling, calyx cupular, bilabiate, 11–21 cm long and 6–12 cm wide, densely lepidote; corolla white to pinkish-lavender or magenta, the throat opening yellow, turning white, tubular-infundibuliform, 5–10 cm long and 1.5–3.2 cm wide at the mouth of tube, the tube 3–5.8 cm long, the lobes 2.2–2.6 cm long, glabrous outside, ciliate, sparsely pubescent within with small mostly unicellular trichomes on throat ridges and gland-tipped trichomes at the point of stamen insertion; stamens didynamous, the thecae divaricate, 2.5–3.5 mm long, the longer filaments 1.4–2.0 cm long, shorter filaments 1.0–1.5 cm long, the staminode 2–6 mm long, inserted 5–10 mm from base of corolla; pistil 1.9–3.2 cm long, the ovary linear, 5–8 mm long and 1 mm wide, densely lepidote, the ovules 2-seriate in each locule; disc tapered-cupular, 2–3 mm long and 3–3.5 mm wide. *Capsule* linear-cylindric, attenuate at both ends, 22–38 cm long and 0.9–1.5 cm wide, lepidote, the calyx usually persistent; seeds 0.7–1.0 cm long and 2.8–4.4 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A widespread tree in tropical wet forest, tropical moist forest, and tropical dry forest, it is also extensively cultivated as an ornamental and its wood is much used for furniture. Altitudinally it reaches 1500 meters. It ranges from southern Mexico to Venezuela. This species flowers mostly during the dry season, occasionally early in the wet season. The wind-dispersed seeds are released mostly in the early wet season in late April and May.

The commercial importance of *Tabebuia rosea* is such that it is usually harvested by timber cruisers before clearing or general lumbering of an area begins. In Panama it is often the fourth tree species after *Swietenia, Cedrela,* and *Bombacopsis* to be removed and is usually the last species to be selectively cut.

For a discussion of the nomenclatural problems of this species see Sandwith (Kew Bull. 1953: 453. 1954), who showed the propriety of using the name *T. rosea.* It has also been widely known as *T. pentaphylla.*

Tabebuia rosea is recognized by its 5-foliolate, lepidote but otherwise completely glabrous leaves.

BOCAS DEL TORO: Punta Róbalo to Robalo River, *Seibert 1564* (MO, US). CANAL ZONE: Barro Colorado Island, *Brown 18* (F); *Croat 4662* (MO, SCZ), *4674, 4884* (both MO), *5436* (MO, SCZ), *5726* (MO), *7771* (MO, SCZ), *7928* (MO), *8184* (MO, SCZ), *8299* (MO), *8394* (MO, SCZ); *Gentry 444* (WIS); *Shattuck 565* (MO), *650* (F, MO), *Standley 40928* (US); *Wetmore et al. 85* (A, F, GH, MO); *Wilson 102* (F, MO). Monte Lirio, *Christopherson 125* (NY, US). Boy Scout road near Madden Lake, *Gentry 2057* (MO). Madden Dam, *Gentry 5067* (MO). Around Culebra, *Pittier 2767* (GH, NY). Las Cascades Plantation near Summit, *Standley 25800* (US). Mount Hope Cemetery, *Standley 28825* (US). Curundu in back of Club house, *Tyson 3657* (SCZ). CHIRIQUÍ: Progreso, *Cooper & Slater 268* (F, US), *311* (NY). COCLÉ: Near El Valle de Antón, *Gentry & Dwyer 3597, 3685* (both MO). Natá, *Seemann 1126* (K). Penonomé and vicinity, *Williams 429* (NY, US). COLÓN: Road to Portobelo, *Gentry 1772* (MO). Tres Brazos sawmill at Icacal between Salud and Boca de Río Indio, *Howell 55* (MO). DARIÉN: Vicinity of Pinogana, *Allen 4287* (G, MO, NY, US). S of Jaqué, *Gentry 4118* (MO). Summit of Cerro Chucula, *Gentry 4243*

(MO). S of La Palma, *Gentry 4291* (MO). El Real, *Gentry 4318, 4579* (both MO). Río Paya from Río Tuira to village of Paya, *Gentry 4390* (MO). Quebrada Sierpe between Ríos Cube and Punusa, *Gentry 4469* (MO). Near Cerro Pirre on Río Parasenico, *Gentry 4694* (MO). HERRERA: S of Ocú, *Gentry 3121* (MO). PANAMÁ: Universidad de Panamá, *Diaz s.n.* (MO, PMA). Vicinity of El Llano, *Duke 5819* (MO). Perlas Islands, Isla Espiritu Santo, *Duke 10456* (MO). Cañitas, *Gentry 1404* (MO). Between El Llano and Chepo, *Gentry 1408* (MO). Cerro Campana above Su-Lin Motel, *Gentry 1827* (MO). Río Pasiga, *Gentry 2194, 2343* (both MO). Río Piragua (Tabardi), *Gentry 2521* (MO). Near Río Espave, *Gentry 3712* (MO). Near last river before Río Partí on trail from Bayano crossing to Santa Fé, *Gentry 3799* (MO). W of El Llano, *Gentry 4962* (MO). Dam site on Río Bayano, *Gentry & Tyson 1648* (MO). Swamp between El Jagua Hunting Club and El Congor Hill, *Hunter & Allen 476* (F, G, K, MO). Perlas Islands, San José Island, *Johnston 519* (GH). Chepo, *Kluge 20* (F, US). E of Río Tocumen, *Standley 26666* (US). Río Tapia, *Standley 28094* (MO, US). SAN BLAS: Vicinity of Puerto Obaldía, *Gentry 1528A* (MO). VERAGUAS: 1–2 mi. above Santa Fé, *Gentry 3039* (MO). Without locality, *Seemann s.n.* (K). WITHOUT LOCALITY: *Hayes 982* (NY). Isthmus of Darien, *Barclay s.n.* (BM, K).

8. **Tabebuia striata** A. Gentry.[9] TYPE: Panama, San Blas, Puerto Obaldía, *Gentry 1484* (MO).—FIG. 36C.

Tree to 15 m tall and 10 cm d.b.h., the bark pale gray, smooth, with a faint sweetish odor when cut, the branches strongly ascending; twigs terete with a large pith, lepidote. *Leaves* simple, opposite, elliptic to narrowly obovate, acute to obtuse, basally cuneate, 21–38 cm long and 6.5–13.3 cm wide, regularly lepidote above and beneath with 2 distinct sizes of scales, somewhat lepidote-glandular at the base of the blade, drying olive with the veins tan, midvein conspicuously raised beneath; petiole 1.2–6 cm long. *Inflorescence* unknown. *Flowers* with the calyx (in fruit) spathaceous, the apex often somewhat split, 2.5–3 cm long and 0.9–1.9 cm wide, densely lepidote, drying gray, conspicuously 5-striate with slightly raised lines; corolla, stamens and pistil unknown. *Capsule* subterete, dehiscing perpendicularly to the septum, 12–25 cm long and 2–2.8 cm wide, the valves coriaceous, densely lepidote, drying gray, the calyx persistent; seeds thin, bialate, 1.1–1.5 cm long and 1.9–2.5 cm wide, the wings short, thin, basally membranaceous at the extreme tip.

A tree of the tropical wet forest, this species is known only from the type locality in extreme eastern Panama almost on the Colombian border. It is locally not uncommon, and seedlings were found at several places on the mountain slopes above Puerto Obaldia.

Although flowers of this species are not known, it is distinct from all other species of the genus. Its simple leaves and lack of pubescence other than lepidote scales relate it to *T. insignis* (Miq.) Sandw. and *T. stenocalyx* Sprague & Stapf. However its leaves are thinner and much longer than in either of these species. Its spathaceously split calyx in fruit differs from that of *T. insignis*. The fruit of *T. stenocalyx* is similar to *T. striata* but narrower, 1.5–2 cm wide (fide Sandwith, 1954). Its calyx also splits spathaceously in fruit but is not so conspicuously striate. Although *T. striata* is close to *T. stenocalyx*, I do not

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[9] *Tabebuia striata* A. Gentry, sp. nov. Arbor ad 15 metros, cortice laevi; folia simplicia obelliptica, cuneata ad basem, lepidota; inflorescentia ignota; calyx (in fructo) spathaceus, dense lepidotus, striatus quinque lineis elevatis; corolla, stamina et pistillum ignota; capsula subteres perlepidota; semina tenuia, bialata.

think the two are the same, especially in view of the latter's distribution (Trinidad, the Guianas, and the Departments of Bolivar and Delta Amacuro in Venezuela). *Romeroa verticillata* Dugand of Colombia also seems related to *T. striata*, especially on the basis of leaves. It differs in a much wider fruit, usually whorled leaves, orbicular seeds with opaque wings, and in lacking a striate calyx.

SAN BLAS: Puerto Obaldía, *Gentry 1484, 1488* (both MO).

37. TANAECIUM

Tanaecium Sw., Nov. Gen. Sp. Pl. 2: 91. 1788. TYPE: *T. jaroba* Sw.

Osmohydrophora Barb. Rodr., Vellosia, ed. 2. 1: 48. 1891. TYPE: *O. nocturna* Barb. Rodr. = *Tanaecium nocturnum* (Barb. Rodr.) Bur. & K. Schum.

Lianas; stems with 8 or 16 phloem arms in cross section; branchlets terete, with or without interpetiolar glandular fields; pseudostipules inconspicuous or lacking. *Leaves* 2–3-foliolate, the terminal leaflet often replaced by a simple tendril; vegetative parts often with a conspicuous almond (cyanide) odor. *Inflorescence* an axillary or terminal raceme or racemose panicle. *Flowers* fragrant, calyx cupular, more or less truncate, sometimes minutely 5-denticulate, often with plate-shaped glands in the upper part; corolla white, elongate-tubular to hypocrateriform, pubescent or glabrous without; stamens usually more or less exserted, anthers glabrous, the thecae straight or arcuate, somewhat divergent; pollen grains single, 3-colpate or irregularly many-porate, the exine finely reticulate; ovary oblong, lepidote, the ovules multiseriate in each locule; disc cupular-pulvinate. *Fruit* an oblong-cylindric capsule, the valves parallel to the septum, thick, woody, not at all compressed, smooth, the median nerve invisible or furrowed, wingless or bialate with brownish irregularly-edged, poorly demarcated membranaceous wings.

Six species of tropical America ranging from Costa Rica and Jamaica to Brazil.

a. Leaves mostly 3-foliolate, the leaflets elliptic, pinnately veined; corolla tube densely puberulous outside; stamens more or less included; seeds thick, woody, wingless; Caribbean coast ..... 1. *T. jaroba*

aa. Leaves 2-foliolate, the leaflets ovate to subrotund, conspicuously 3-veined from base; corolla tube glabrate outside; stamens mostly exserted; seeds bialate with brownish membranaceous wings; eastern Panama ..... 2. *T. nocturnum*

1. **Tanaecium jaroba** Sw., Nov. Gen. Sp. Pl. 92. 1788; Fl. Ind. Occ. 2: 1050, *tab. 20, fig 1.* 1800. TYPE: Jamaica (not seen).

T. albiflora DC., Prodr. 9: 245. 1845. TYPE: Based on *T. jaroba* Sw.
T. exsertum Griseb., Fl. Brit. W. Ind. Is. 450. TYPE: Jamaica, *Mench 1070* (K).

Liana; branchlets terete, the nodes without pseudostipules, interpetiolar glandular fields mostly lacking or inconspicuous, if present relatively small. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets elliptic, acute or rounded, truncate or rounded at the base, 8–10 cm long and 4–6 cm

wide, pinnately veined with 5–7 lateral veins on a side, drying grayish-green, the veins beneath beige, glabrous except for a few long trichomes at the extreme base of the midvein above or puberulous with simple trichomes along the veins beneath; tendril simple; petiole 5–6 cm long, petiolules 1–3 cm long, grooved on the upper surface, pubescent with scattered long trichomes along the groove, otherwise lepidote. *Inflorescence* a terminal raceme on a short lateral branch; pedicels 1.3–2.4 cm long. *Flowers* with the calyx cupular, subtruncate or minutely 5-denticulate, more or less ciliate, glandular-spotted but mostly glabrous with some plate-shaped glands on the apical part; corolla white, elongate-tubular, expanded apically, 18–20 cm long and 1.2–1.7 cm wide at the mouth, the tube 14–17 cm long, the lobes 2–2.8 cm long; densely glandular-puberulous outside, less densely glandular-lepidote and glandular-puberulous on the lobes, more or less ciliate, tube mostly glabrous inside; stamens didynamous, the anthers half-exserted, the thecae 5–6 mm long, the longer filaments ca. 2.8 cm long, shorter filaments ca. 1.5 cm long, the staminode 5 mm long, inserted 11–17 cm above the base of the corolla tube; pistil 16–17 cm long, the ovary oblong, tetragonal, 1.5–2 mm long and ca. 1 mm wide, ovules ca. 6-seriate in each locule; disc cupular-pulvinate, 1.5–2 mm long and 2 mm wide. *Capsule* elliptic-oblong, 14–22 cm long and 6–11 cm wide, 6–8 cm thick (*Elias 1306* (US), *Dugand & Jaramillo 3500A* (US), both from Colombia), brown with paler lenticellate flecks, glabrous or with a few lepidote scales, the valves woody, convex; seeds angular, woody, wingless but with a sharp edge on 3 sides 2.5–3.3 cm long and 3.0–3.2 cm wide, the hilum terminal and at right angles to the seed body.

No Panamanian collections of this species have been seen, but it is probably a member of the flora of Panama. I have collected it in Costa Rica only a few miles from the Panamanian border, and it is also known from Colombia.

Vegetatively it resembles *Arrabidaea* in having 3-foliolate leaves, a simple tendril, an interpetiolar glandular field, and a stem cross section with 4 phloem arms. Its strongly raised venation on the leaf undersides, the small size of its interpetiolar glandular fields, and the swampy habitat separate it from species of *Arrabidaea*.

A plant of lowland swampy areas along the Caribbean coast, *T. jaroba* occurs in regions of tropical moist forest but is probably restricted more by local edaphic than by climatic factors. It ranges from Costa Rica to Venezuela and also to Jamaica. It is only doubtfully distinct from the West Indian and Venezuelan *T. crucigerum* Seem.

Presumably moth pollinated, it was collected in flower in Costa Rica in late May. Its thick, wingless seeds are water-dispersed, correlating with its swampy habitat and more or less circum-Caribbean distribution.

2. **Tanaecium nocturnum** (Barb. Rodr.) Bur. & K. Schum. *in* Mart. Fl. Bras. 8(2): 185. 1896.—Fig 37.

Osmohydrophora nocturna Barb. Rodr., Vellosia, ed. 2. 1: 49. 1891; 3: *tab.* 8–9. 1891. TYPE: Brazil, Amazonas, *Barbosa Rodriguez s.n.* (not seen).

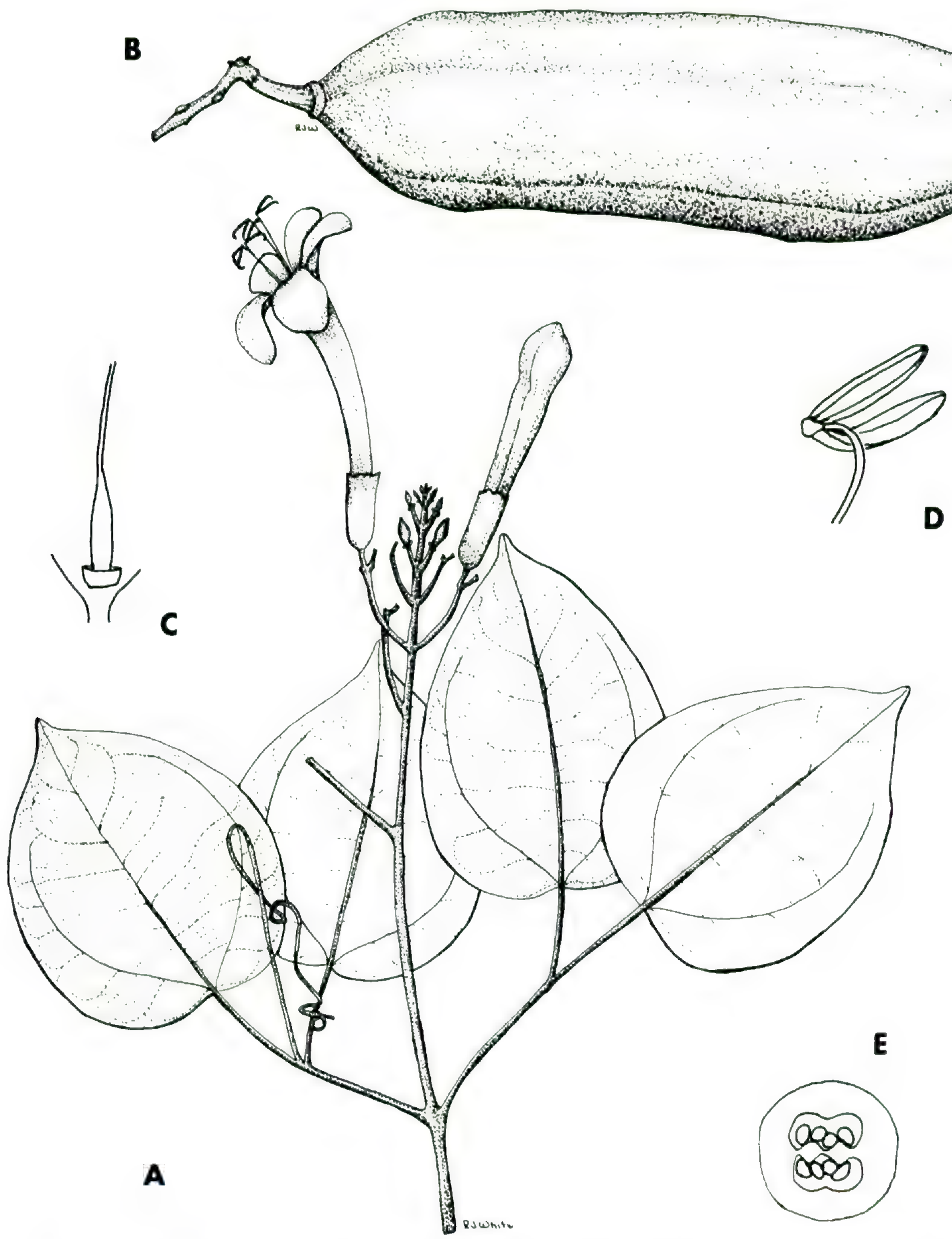


FIGURE 37. *Tannaecium nocturnum* (Barb. Rodr.) Bur. & K. Schum.—A. Habit (× ½). [After *Tyson et al. 4808*, *Bristan 1061*, and *Gentry 4543* (all MO).]—B. Fruit (× ½). [After *Gentry & Clewell 6926* (MO).]—C. Ovary and disc (× 1½).—D. Anther (× 2½).—E. Ovary cross section (× 8½). [After fresh material of *Gentry* 5233, Colombia.]

Liana to at least 5 cm in diameter, the bark smooth, pale gray; stem with 8(–16) arms in cross section; vegetative parts with a conspicuous almond odor; branchlets subterete, finely longitudinally striate, elenticellate, lepidote, the nodes without interpetiolar glandular fields or ridges; pseudostipules lacking. *Leaves* 2-foliolate, sometimes with a tendril; leaflets ovate to subrotund, acuminate to acute, rounded to slightly cordate, 8.8–16.0 cm long and 5–12.5 cm

wide, membranaceous, palmately veined at the base, the basal pair of lateral nerves conspicuous, strongly arcuate, with axillary glandular fields beneath, other secondary veins inconspicuous, mostly glabrous above and basally lepidote, beneath glabrous to slightly lepidote; tendril simple, 7–18 cm long; petiole and petiolules thinly lepidote, petiolules 2.5–7.7 cm long, apically glandular; petiole 2.7–7.5 cm long. *Inflorescence* a terminal racemose panicle, the branches lepidote. *Flowers* fragrant, calyx tubular, more or less truncate, 16–18 mm long and 8–9 mm wide, scattered lepidote with glands; corolla white, elongate-tubular, somewhat curved, 8.5–13.0 cm long and 0.7–1.6 cm wide at the mouth, the tube 6.6–9.5 cm long, the lobes 1.2–2.4 cm long, glabrous to sparsely glandular-lepidote outside, the lobes densely glandular-lepidote inside, the tube glabrous; stamens exserted, anther thecae somewhat divergent, arcuate, 6–10 mm long, the filaments about equal, 4–5 cm long, the staminode 2–3 mm long, inserted 4.7–7.2 cm from base of the corolla tube; pistil 7.8–9 cm long; ovary elongate-oblong, lepidote, 6–7 mm long and 2 mm wide, the ovules 4–6-seriate in each locule; disc pulvinate, 1 mm long and 3–4 mm wide. *Capsule* ovoid-cylindrical, 12.7–20 cm long and 4–4.8 cm in diameter, 3.5–4 cm thick, the surface impressed-lepidote, drying light brown; seeds 1.2–2.3 cm long and 4.4–7.5 cm wide, the wings membranaceous but brownish, irregular-edged, not sharply demarcated from the seed body.

A vine of the tropical moist forest and tropical wet forest, it is known in Central America only from Darién Province. To the south it ranges to Amazonian Brazil. It was previously reported only from the drainage of the Amazon and northeastern Colombia. It flowers during the early wet season from May through July. Seeds are released during the dry season and are mostly wind-dispersed; however the thickness of the central portion of the seed suggests an intermediate stage in the evolution of water-dispersed seeds.

Tanaecium nocturnum is recognized by its pronounced, arcuate basal pair of lateral veins, the almond odor, or by its smooth bark, which is reminiscent of that of *Carpinus caroliniana*. The long, tubular, white flower of *Tanaecium* is almost unique among the Bignonieae and strikingly convergent with the flowers of *Tabebuia stenocalyx* and *Ekmanianthe* of the Tecomeae. The oblong sausage-shaped fruit is also distinctive in the Bignonieae though clearly related to the fruit of *Ceratophytum*. The superficial similarity of the fruit of *Tanaecium* to that of *Crescentia* of the Crescentieae led to much confusion among early taxonomists as to its tribal affiliation.

Vines of this genus contain enough cyanide (Dugand, Caldasia 1(5): 29–35. 1942) to be poisonous to livestock. The cut stems or crushed leaves of *T. nocturnum* give off a strong almond smell, and the plant is considered to have aphrodisiacal properties by the Choco Indians. They maintain that a gift of leaves of this plant to a girl will cause her to fall in love with the giver, or, in a more complicated ritual, that when a handkerchief is scented with the juice of this vine and presented to a girl, she will reciprocate the suitor's attentions within three days.

DARIÉN: Between Quebrada Venado and Peje Swamp on headwaters of Río Tuqueza, *Bristan 1061* (MO, SCZ). Río Pirre, *Bristan 1478, 1501* (both MO). Río Tuira between Ríos Paya and Aspavé, *Gentry 4399* (MO). El Real, *Gentry 4543* (MO). Near Cerro Pirre on Río Parasenico, *Gentry 4684* (MO). Río Pirre near village of Pirre, *Gentry & Clewell 6926* (MO). E of Santa Fé, *Tyson et al. 4808* (MO, SCZ). Cana and vicinity, *Williams 982* (NY).

38. TECOMA

Tecoma Juss., Gen. 139. 1789. LECTOTYPE: *T. stans* (L.) Juss. *ex* H.B.K.

Stenolobium D. Don, Edinburgh Phil. Jour. 9: 264. 1823. TYPE: *S. castanifolium* D. Don = *T. castanifolia* (D. Don) Melch.

Kokoschkinia Turcz., Bull. Soc. Imp. Naturalistes Moscou 2: 33, *tab. 2.* 1849. TYPE: *T. gaudichaudi* DC. (fide *Index Kewensis*).

Shrubs or small *trees*. *Leaves* simple, 3-foliolate or imparipinnately compound, the leaflets serrate. *Inflorescence* a terminal raceme or racemose panicle. *Flowers* with the calyx cupular, with 5 shallow, often apiculate, deltoid lobes, corolla yellow or orangish, tubular-campanulate to narrowly tubular-infundibuliform, glabrous outside; stamens exserted or included, the anthers variously divergent, glabrous or pilose; pollen grains single, oblong, 3-colpate, the exine microreticulate; ovary narrowly cylindric, lepidote, the ovules 2-seriate in each locule; disc cupular-pulvinate. *Fruit* a linear capsule, somewhat compressed parallel to the septum but dehiscing perpendicularly to it, the valves smooth, more or less glabrous; seeds thin, bialate, the wings hyaline-membranaceous, sharply demarcated from the seed body.

About a dozen species ranging from extreme southern Arizona and southern Florida through tropical America to northern Argentina, especially in the Andes.

1. **Tecoma stans** (L.) Juss. *ex* H.B.K., Nov. Gen. Sp. Pl. 3: 144. 1819.—FIG. 38.

Bignonia stans L., Sp. Pl., ed. 2. 2: 871. 1763. TYPE: (not seen).

Tecoma mollis H.B.K., Nov. Gen. Sp. Pl. 3: 144. 1819. TYPE: Mexico, Guanaxuato, *Humboldt & Bonpland s.n.* (P).

Tecoma incisa Sweet, Hort. Brit., ed. 1. 284. 1827, nomen nudum. TYPE: Trinidad (not seen).

Bignonia frutescens Mill. *ex* DC., Prodr. 9: 224. 1845, pro syn.

B. incisa Hort. *ex* DC., Prodr. 9: 224. 1845, pro syn.

Tecoma stans var. *apiifolia* Hort. *ex* DC., Prodr. 9: 224. 1845. TYPE: Guadeloupe, *Bertero s.n.* (G-DC).

T. stans var. *velutina* DC., Prodr. 9: 224. 1845. SYNTYPES: Cultivated in Hort. Madrid, from Mexico (G-DC); cultivated in Jard. Sarme (G-DC).

Stenolobium molle (H.B.K.) Seem., Jour. Bot. 1: 91. 1863.

S. stans (L.) Seem., Jour. Bot. 1: 88. 1863.

S. stans var. *pinnata* Seem., Jour. Bot. 1: 89. 1863. TYPE: Panama, *Seemann 558* (BM).

S. stans var. *apiifolium* (DC.) Seem., Jour. Bot. 1: 89. 1863.

Gelseminum molle (H.B.K.) Kuntze, Rev. Gen. 2: 480. 1891.

G. stans (L.) Kuntze, Rev. Gen. 2: 479. 1891.

Stenolobium incisum Rose & Standl., Contr. U. S. Natl. Herb. 26: 174. 1913. TYPE: Mexico, Chihuahua, *Pringle 960* (US).

Tecoma stans var. *angustatum* Rehder, Mitt. Deutsch. Dendrol. Ges. 1915: 227. 1915. TYPE: United States, Texas, El Paso, *Jones 4187* (A).

Stenolobium quinquejugum Loes., Fedde Repert. 16: 211. 1919. TYPE: Mexico, El Calabaral, *Langlasse 478* (K).

S. tronadora Loes., Fedde Repert. 16: 210. 1919. LECTOTYPE: Mexico, Durango, *Palmer 131* (MO).

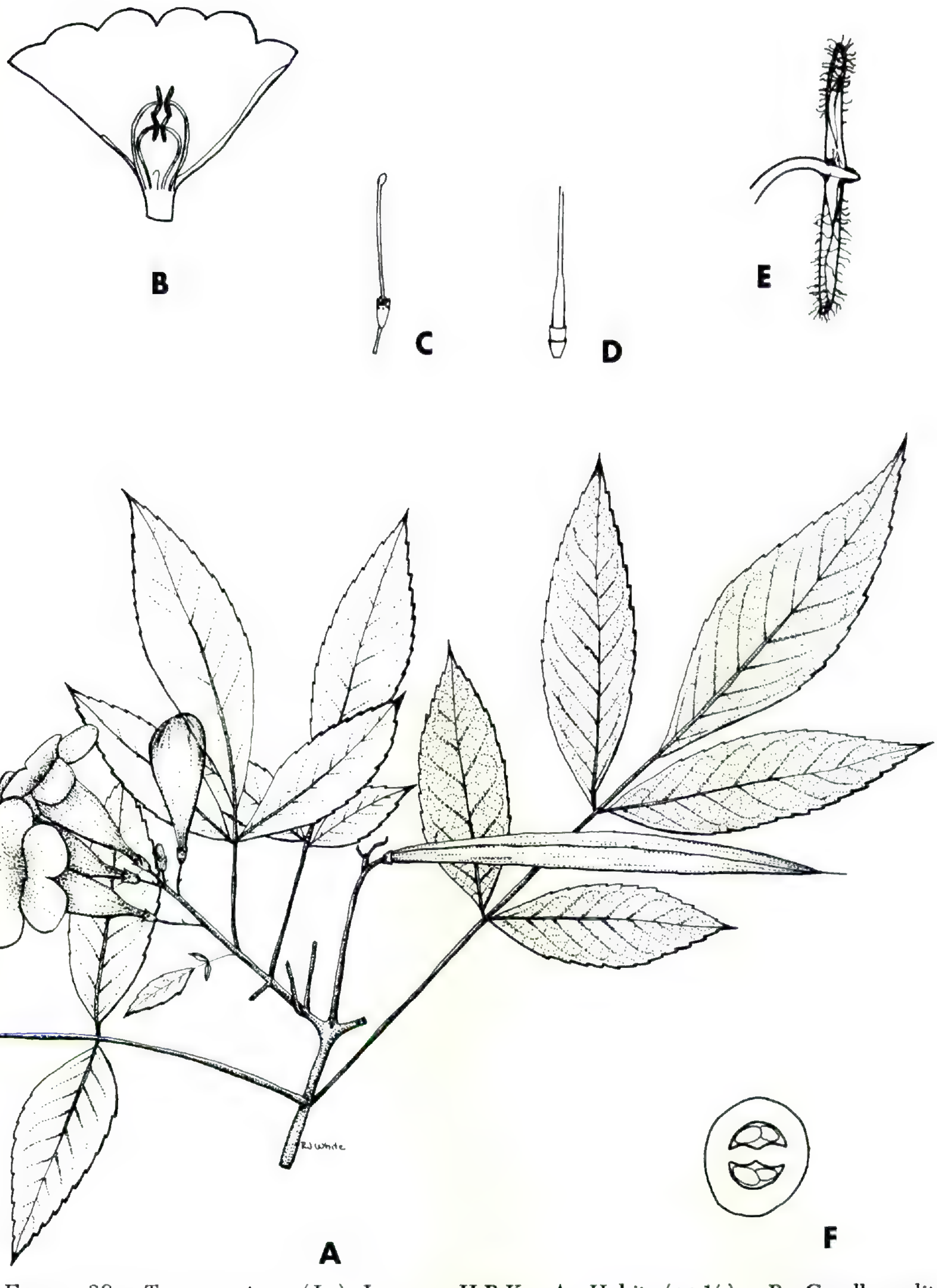


FIGURE 38. *Tecoma stans* (L.) Juss. *ex* H.B.K.—A. Habit (× ½).—B. Corolla split open (× ½).—C. Calyx and pistil (× ½).—D. Ovary and disc (× 1½).—E. Anther (× 5).—F. Ovary cross section (× 12½). [After *Gentry* 2895 (MO).]

Shrub or small *tree* to 10 m tall and 25 cm d.b.h., the bark dark and ridged; twigs lepidote and irregularly subpuberulent, more or less terete, drying dark brown when young, light brown when mature. *Leaves* (in Panama) imparipinnately compound, 3–9-foliolate, the first pair of leaves on a new branch

often simple or 1-foliolate, the leaflets opposite, serrate, lanceolate, apically acute, basally cuneate, the terminal leaflet often attenuate, 2.4–15 cm long and 0.8–6 cm wide, progressively larger distally, somewhat lepidote above and beneath, simple puberulous on the midvein above and beneath, often puberulous beneath at the base of the secondary nerves and sometimes on the leaf surface, especially in the vein axils; petiolules of the lateral leaflets lacking or to 2 mm long, the terminal leaflet 4–20 mm long; petiole 1–9 cm long, rachis lacking (in 3-foliolate leaves), to 8 cm long, petiole and rachis slightly lepidote, puberulous at the leaflet bases. *Inflorescence* a terminal or subterminal raceme of to 20 flowers, only a few flowers opening at a time; pedicels and inflorescence rachis lepidote. *Flowers* fragrant with a sweet odor similar to vanilla; calyx elongate-cupular, evenly 5-dentate, the teeth ca. 1 mm long and usually apiculate, 3–7 mm long and 3–4 mm wide, somewhat lepidote throughout, ciliate with conspicuous sunken submarginal glands; corolla yellow with 7 reddish lines in the throat, 2 additional fainter red lines on top of throat ridges and a short faint line at the base of the 2 upper lobes, tubular-campanulate above a narrowed base 0.9–1.0 cm long, 3.5–5.8 cm long and 1.2–2.4 cm wide at the mouth, the tube 3.0–4.3 cm long, the lobes 1.0–1.6 cm long, glabrous outside with a glandular epidermis, inside glabrous except for gland-tipped trichomes at the level of stamen insertion and twisted trichomes in sinuses and on throat ridges; stamens didynamous, the anther thecae divaricate, 3.5 mm long, pubescent with twisted, simple, multicellular trichomes, the longer filaments 2.1–2.4 cm long, shorter filaments 1.5–1.8 cm long, the staminode 4–5 mm long, inserted 8–9 mm from the base of the tube; pistil 3.1–3.4 cm long, ovary narrowly cylindric, 3 mm long and 1 mm wide, glandular-lepidote, the ovules 2-seriate in each locule; disc cupular-pulvinate, 1 mm long and 1 mm wide. *Capsule* linear, tapering at the ends, subterete when fresh, 7–21 cm long and 5–7 mm wide, surface lenticellate, more or less glabrous, sometimes slightly and inconspicuously lepidote; seeds 3–5 mm long and 2.4–2.7 cm wide, wings hyaline-membranaceous, sharply demarcated from the seed body.

A characteristic plant of the premontane moist forest and also occurring sparsely and locally in drier parts of the tropical moist forest, *T. stans* is cultivated frequently throughout the tropics and subtropics. Extremely wide-ranging, it occurs naturally from southern Florida and southern Arizona through the West Indies and Central America to northern Argentina.

This species flowers mostly during the early dry season from December to February, also producing a few sporadic flowers throughout the year. Fruit is produced mostly in the dry season.

Numerous varieties of this phenotypically plastic species have been named. In Panama and Costa Rica the populations are relatively homogeneous, and it is best to treat the plant as a single species without designation of varieties.

CANAL ZONE: Fort Kobbe, *Allen 2019* (GH, MO, US). Along K-2 N of Cocoli, *Croat 9171* (MO, SCZ). Culebra Island, *Duke 4633* (MO, US), *4634* (MO). Madden Dam, *Dwyer 3060* (MO). Summit of Cerro Luisa, *Gentry 1402* (MO). Below Sosa Hill, *Gentry 2895* (MO). Farfan beach road, *Gentry & Dwyer 3547* (MO). SE of junction of K-2 with K-15 on K-2, *Graham 315* (GH). Between Farfan Beach and Palo Seco, *Hunter & Allen 442* (MO,

U, US); *Lewis et al. 55* (GH, MO). Bella Vista, *Salvoza 1009* (A). Balboa, *Standley 30906* (US). Farfan Beach area, *Tyson 1813* (MO, SCZ). Fort Amador on causeway and islands, *Tyson 2021* (MO, SCZ). Ancón below MARU research labs, *Tyson 2798* (MO, SCZ, US). La Boca, *Williams 618* (US). Fort Grant, *Woodson et al. 1552* (A, MO). CHIRIQUÍ: Boquete, *Sanchez 9* (MO, PMA). COCLÉ: Santa Clara Beach, *D'Arcy & Croat 4096* (MO, SCZ); *Woodson et al. 1704* (A, MO). COLÓN: Santa Rita Trail, *Cowell 107* (US). 2 km de la carretera Transistmica, a mas o menos 1500 m del Río Chagres, *Rosas 31* (MO). DARIÉN: Vicinity of Vera Cruz, *Duke 6062* (MO, SCZ). Isla Rosero in Golfo de San Miguel, *Gentry 3983* (MO). Second large point just before Punta Alegre NE of Garachiné, *Gentry 4057* (MO). LOS SANTOS: Playa de La Concepción, *Burch et al. 1259* (GH, MO, PMA, SCZ). Pedasí, *Dwyer 2488* (MO). Road from Macaracas to Chitré, *Tyson et al. 3152* (MO, SCZ). PANAMÁ: Ruins of Franciscan Convent, *Celestine, 31* (US). Perlas Islands, San José Island, *Correa 99* (SCZ); *Duke 12527* (MO); *Erlanson 75* (GH, US), *126* (GH); *Johnston 547* (GH, MO); *Tyson & Loftin 5054* (CRU, MO, SCZ). Perlas Islands, Isla del Rey, *Duke 9554* (MO). Perlas Islands, Isla Espiritu Santo, *Duke 10443* (MO). Facultad de Ciencias de la Universidad de Panamá, *Escobar 27* (PMA). Vera Cruz, *Lewis et al. 3007* (MO, SCZ). Vicinity of Panamá, *MacBride 2622* (US). Cerca de la Costa, *Mejia 10* (MO, PMA). Bella Vista, *Standley 25402* (A, US). In Chorrera, *Tyson 5935* (SCZ). WITHOUT LOCALITY: *Cuming 1096* (BM); *Seemann 558* (BM).

39. TECOMARIA

Tecomaria Spach, Hist. Nat. Vég. Phan. 9: 137. 1840. TYPE: *T. capensis* (Thunb.) Spach.

Shrubs or subshrubs. *Leaves* imparipinnately compound, usually 9–11-foliolate, the leaflets serrate. *Inflorescence* a raceme or racemose panicle. *Flowers* with the calyx cupular, 5-toothed; corolla orange to scarlet, tubular, curved; stamens exserted, the thecae more or less parallel, only slightly divergent, attached to the filament ca. 1 mm from the fused end of the thecae. *Fruit* a linear capsule, dehiscing perpendicularly to the septum; the seeds flat, membranaceous-winged.

Two species of southern and eastern Africa, widely cultivated in the tropics and subtropics.

1. **Tecomaria capensis** (Thunb.) Spach, Hist. Nat. Vég. Phan. 9: 137. 1840.

Bignonia capensis Thunb., Prodr. 105. 1794–1800. TYPE: (not seen).
Tecoma capensis (Thunb.) Lindl., Bot. Reg. *tab. 1117*. 1827.
Tecomaria krebsii Kl. *in* Peters, Reise Mossamb. Bot. 193. 1862–1864. TYPE: (not seen).
T. petersii Kl. *in* Peters, Reise Mossamb. Bot. 192. 1862–1864. TYPE: (not seen).

Shrub or subshrub, the branches flexuous. *Leaves* opposite, pinnately compound, usually 7–11-foliolate; the leaflets elliptic to suborbicular, apically and basally rounded or abruptly cuneate, sessile, ca. 1.5 cm long and 1.0 cm wide, serrate, membranaceous, puberulous at least along main veins, the axils usually with tufts of branched trichomes. *Inflorescence* a raceme or racemose panicle. *Flowers* with the calyx cupular, 5-toothed, 5–7 mm long and 4–5 mm wide, more or less puberulous, cilate with scattered plate-shaped glands in the upper half; corolla orange to orange-scarlet, tubular, curved, 3.5–5 cm long and 0.6–0.7 cm wide at the mouth, mostly glabrous, the lobes ciliate; stamens more or less equal in length, anthers exserted, the thecae ca. 3 mm long, slightly divergent for ½–⅔ of their length, the slender filament attached ca. 1 mm

from the fused end of the thecae; pistil 5.5–6.5 cm long, the ovary oblong, glabrous; disc cupular-pulvinate. *Fruit* rarely set in Central America, the capsule linear, 5–11 cm long and 7–8 mm wide; seeds in two rows, thin, bialate with hyaline membranaceous wings.

Native to South Africa, *T. capensis* is commonly cultivated in the subtropics and at higher altitudes in the tropics. Reported by Standley as cultivated frequently in Central America including Costa Rica, collections have not been seen from Panama, but it is certainly to be expected. This plant is recognized by its pinnately compound leaves and narrow tubular orange-red flowers with strongly exserted anthers.

40. TOURRETTIA

Tourrettia Fougeroux, Mém. Acad. Paris 1784: 205. 1787; corr. Schreber Gen. 2: 406. 1791, orth. et nom. cons. TYPE: *T. lappacea* (L'Hér.) Willd.

Dombeya L'Hér., Stirp. Nov. 33. 1786, nom. rej. TYPE: *D. lappacea* L'Hér. = *T. lappacea* (L'Hér.) Willd.
Medica Cothenius, Disp. Veg. 7. 1790, fide *Index Kewensis.*

Herbaceous *vines;* branchlets angled, nodes without interpetiolar glandular fields; pseudostipules lacking. *Leaves* opposite, 2–3-ternate, often with a trifid, dichotomously branching tendril, the leaflets serrate and often more or less subdivided. *Inflorescence* a terminal spike-like raceme, the upper flowers sterile and caducous. *Flowers* with the calyx red, bilobed, caducous; corolla tubular, bilabiate, shorter than the calyx, pubescent at least toward the tip; stamens 4, staminode absent, the anthers glabrous; pollen grains single, 3-colpate, the exine finely granular; ovary ovoid, densely short-echinate; disc annular. *Fruit* an uncompressed, ovoid, septicidally dehiscing capsule, usually not splitting to the base, densely echinate with uncate spines; seeds small, thin, with a narrow, hyaline-membranaceous wing.

One species of upland areas of continental tropical America ranging from Guatemala to Argentina.

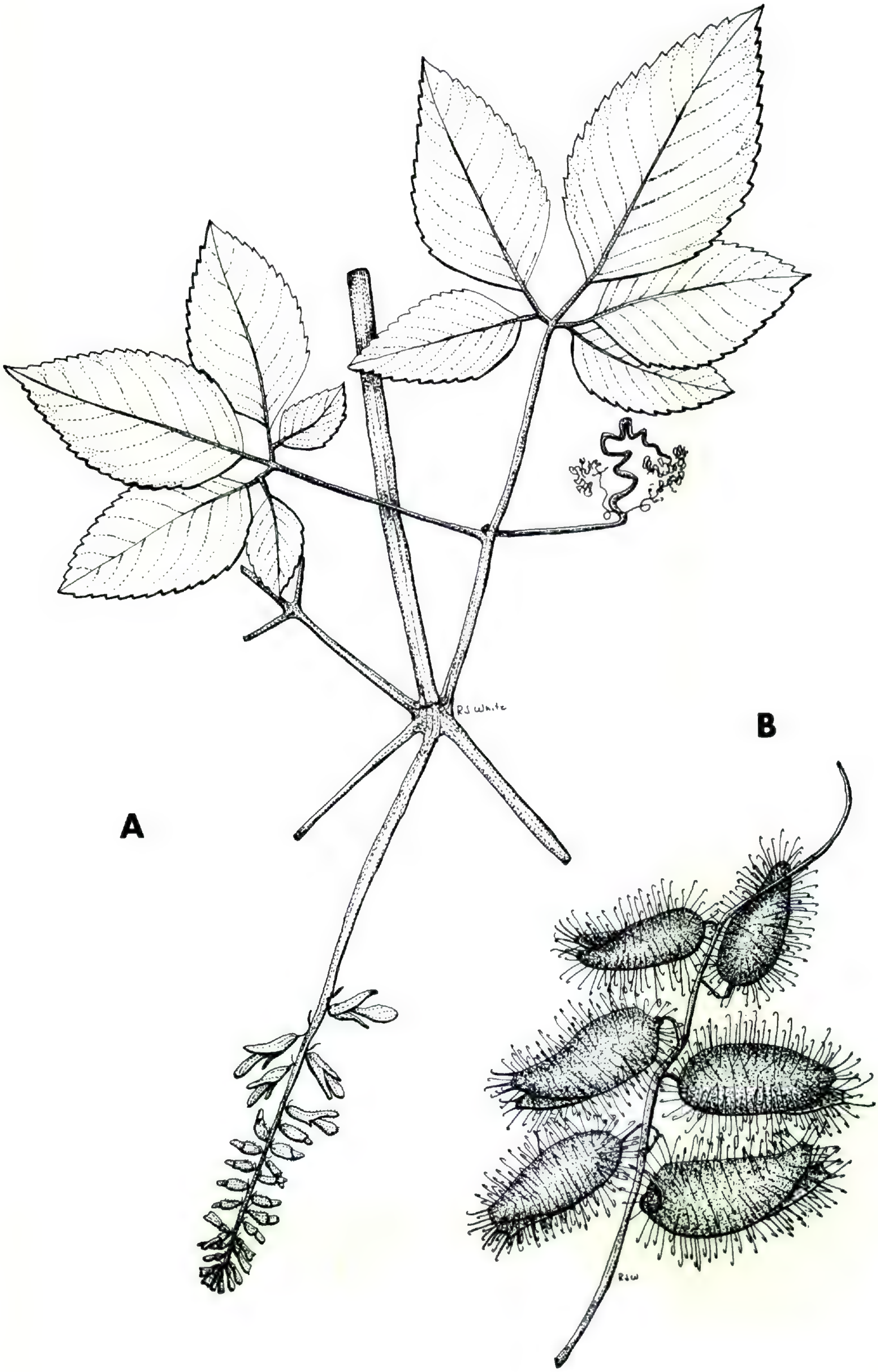
1. **Tourrettia lappacea** (L'Hér.) Willd. *in* L., Sp. Pl., ed. 4. 3: 263. 1801.—FIG. 39.

Dombeya lappacea L'Hér., Stirp. Nov. 33, *pl. 17.* 1785. TYPE: Peru, *Pavon s.n.* (BM).
Tourretia volubilis J. F. Gmel., Syst. Nat. 2: 940. 1791. TYPE: (not seen).

Herbaceous *vine*, the branchlets tetragonal. *Leaves* opposite, biternate with a subterminal, finely branched, spirally coiling tendril, the leaflets membranaceous, glabrous, conspicuously and unevenly serrate, 3–8 cm long and 1.5–5 cm wide, the lateral pair of a ternation often divided to base. *Inflorescence*

→

FIGURE 39. *Tourrettia lappacea* (L'Her.) Willd.—A. Habit (× 3/5). [After *White 23* and *D'Arcy 6637* (both MO).]—B. Fruit (× 3/5). [After *Woodson et al. 1116* (MO).]


A
B
RJ White
RJW

spicate but with short pedicels, narrowly bracteate, the bracts scarlet, the terminal flowers mostly sterile with bright red calyces. *Flowers* with the calyx of fertile flowers 1.3–1.5 cm long, somewhat hirsute, deeply 2-parted more than half its length, the upper lobe long-acuminate, the lower lobe acute, the limbs red; corolla purplish to greenish, tubular, 1.6–1.8 cm long and apically 3–5 cm wide, bilabiate, the tube 1–1.1 cm long, the lip 6–8 cm long, all lobes fused forming a protective hood over the anthers, this open below, pubescent outside, mostly glabrous inside, pubescent at the base of the stamens; stamens 4, the anther thecae divaricate, glabrous, 1–2 mm long, shorter filaments 8–9 mm long, longer filaments 9–11 mm long, staminode absent, inserted 7–8 mm from the base of the tube; pistil 1.4–1.5 cm long, the ovary ovoid, densely short-tuberculate with thick, single-celled trichomes, 2.5–3 mm long and 1.5 mm wide, 4-celled, the ovules uniseriate in each locule; disc cupular-membranaceous, 1 mm long and 1.5 mm wide; capsule ovoid, somewhat woody, ca. 3.5 cm by 1.7 cm, strongly echinate with long spines to 1 cm long with recurved tips and shorter straight spines, 2-valved, apically septicidally dehiscent, often not splitting to base; seeds thin, flat, 6–7 mm long and 4–5 mm wide, the dark brown body encircled by a narrow brown almost membranaceous wing.

This species is a plant of upper elevations from 600 m to 1800 m. It occurs in the wet or moist premontane and lower montane regions from Guatemala to Peru and in the Andes east to just across the Venezuelan border. The fruits are burr-like and are probably epizoochorous with the seeds shaking a few at a time out of the partially opened capsule.

The relationships of this monotypic genus are not clear. It is perhaps closer to the Pedaliaceae than to the Bignoniaceae, but its compound leaves, tendrils, and winged seeds have led to usual placement in the latter family.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio in upper valley of Río Chiriquí Viejo, *Allen 1477* (GH, MO). E side of Cerro Pando, *D'Arcy 6637* (C, K, MO, P, UCWI). Cerro Punta, *Graham 275* (GH). Vicinity of Boquete, *Lewis et al. 372* (GH, MO, US); *Maurice 725* (US); *Pittier 7001* (US). Río Chiriquí Viejo valley near El Volcán, *White 23* (GH, MO). Finca Lerida to Boquete, *Woodson et al. 1116* (A, MO, NY); *Woodson & Schery 237* (GH, MO, US).

41. TYNNANTHUS

Tynnanthus Miers, Proc. Roy. Hort. Soc. 3: 193. 1863. LECTOTYPE: *T. fasciculatus* (Vell.) Miers.

Schizopsis Bur., Mon. Bign. 44. 1864. TYPE: *S. labiata* (Cham.) Bur. = *Tynnanthus labiatus* (Cham.) Miers.

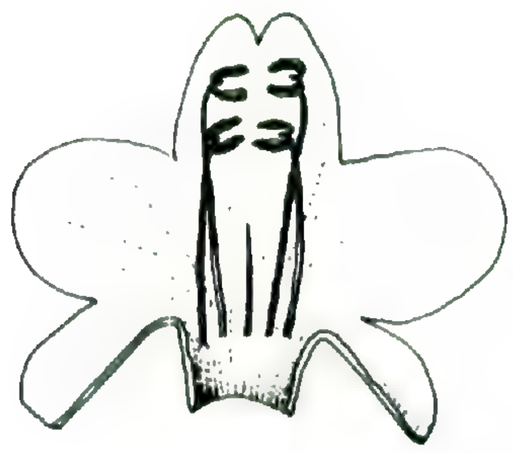
Lianas, perhaps small trees, stems with 4 phloem arms in cross section; branchlets terete to subtetragonal without interpetiolar glandular fields, often with a ridge between opposite petioles; pseudostipules lacking or foliaceous but early deciduous. *Leaves* 2–3-foliolate, the terminal leaflet often replaced by a simple or trifid tendril. *Inflorescence* an open or contracted axillary or terminal panicle. *Flowers* with the calyx small, cupular, subtruncate, usually 5-denticulate or 5-setate; corolla white, often tiny, more or less infundibuliform,

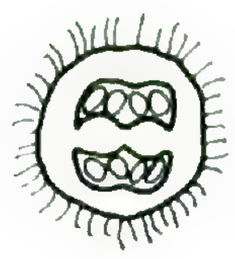
bilabiately split about half its length, pubescent outside; anthers glabrous, subexserted, the thecae divaricate, bent at the middle; pollen grains 3-colpate, the exine smooth; ovary conical, densely pubescent, the ovules 2–4-seriate in each locule. *Fruit* a more or less compressed linear capsule, the valves parallel to the septum, flat with a slightly or conspicuously raised margin; seeds flat, bialate with hyaline-membranaceous wings.

About 12 species of tropical America ranging from southern Mexico and the West Indies to Brazil and Bolivia.

1. **Tynnanthus croatianus** A. Gentry, Ann. Missouri Bot. Gard. 58: 93. 1971. TYPE: Panama, Canal Zone, *Croat 11927* (MO, SCZ).—FIG. 40.

Liana, the stems with 4 phloem arms in cross section, the pith conspicuously 4-angled; branchlets tetragonal, becoming subterete, finely striate, becoming noticeably lenticellate with age, young twigs more or less puberulous, the nodes without interpetiolar glands or pseudostipules, vegetative parts with odor of cloves. *Leaves* 3-foliolate, or 2-foliolate with a tendril or tendril scars; leaflets membranaceous, papillose on both surfaces with scattered lepidote scales especially above, minutely puberulous below mostly on and near nerves and above more or less glabrescently so over whole surface, drying light green to yellowish with distinct yellow to reddish-brown reticulation beneath, darker green to brownish above, the terminal leaflet when present broadly ovate, obtusely acuminate, truncate to broadly cuneate, 5.5–12 cm long and 3.7–8 cm wide, the lateral leaflets broadly ovate, obtusely acuminate, more or less asymmetrically truncate or subcordate on one side at the base, 3.9–10 cm long and 2.7–6 cm wide; terminal petiolule 1.5–3.3 cm long, laterals 0.6–2.5 cm long, the petiole 1.4–7.5 cm long, drying dark reddish; tendril strongly trifid; 11–15 cm long to branching, the 3 arms 1.0–2.2 cm long. *Inflorescence* a small, usually axillary panicle, 3–8 cm long and 2–6 cm wide, the branches strongly puberulous. *Flowers* sweetly aromatic with odor similar to lilacs, calyx cupular, puberulous, eglandular, truncate or minutely sub-denticulate, 3–4 mm long and 3–4 mm wide; corolla white with 2 yellow lines in the throat; bilabiate, 1.2–2 cm long, split about half its length, the 2 upper lobes almost fused, the 3 lower lobes 4–9 mm long, puberulous outside, inside pubescent on lower 3 lobes, margins of upper 2 lobes, at the base of the lower side of the tube and sparsely elsewhere, glabrous at the point of stamen insertion; stamens didynamous, the anther thecae 1.5 mm long, divaricate, twisted near the base and reflexed forward, the connective extended 0.3 mm beyond point of anther attachment, the longer filaments 1.0–1.2 cm long, shorter filaments 0.9–1.0 cm long, the staminode 0.5 cm long, inserted 2 mm from the base of corolla tube; pistil 16–17 mm long, the stigma small, bilamellate, 1 mm long, the style puberulous, the ovary conical 1.5–2 mm long and 1 mm wide at the base, densely puberulous, the ovules 4-seriate in each locule at the bottom of the ovary and 2-seriate at the top; disc reduced, shortly cupuliform, densely pubescent on the margin. *Capsule* linear, acuminate, flattened, 25–35 cm long and 0.8–1.2 cm





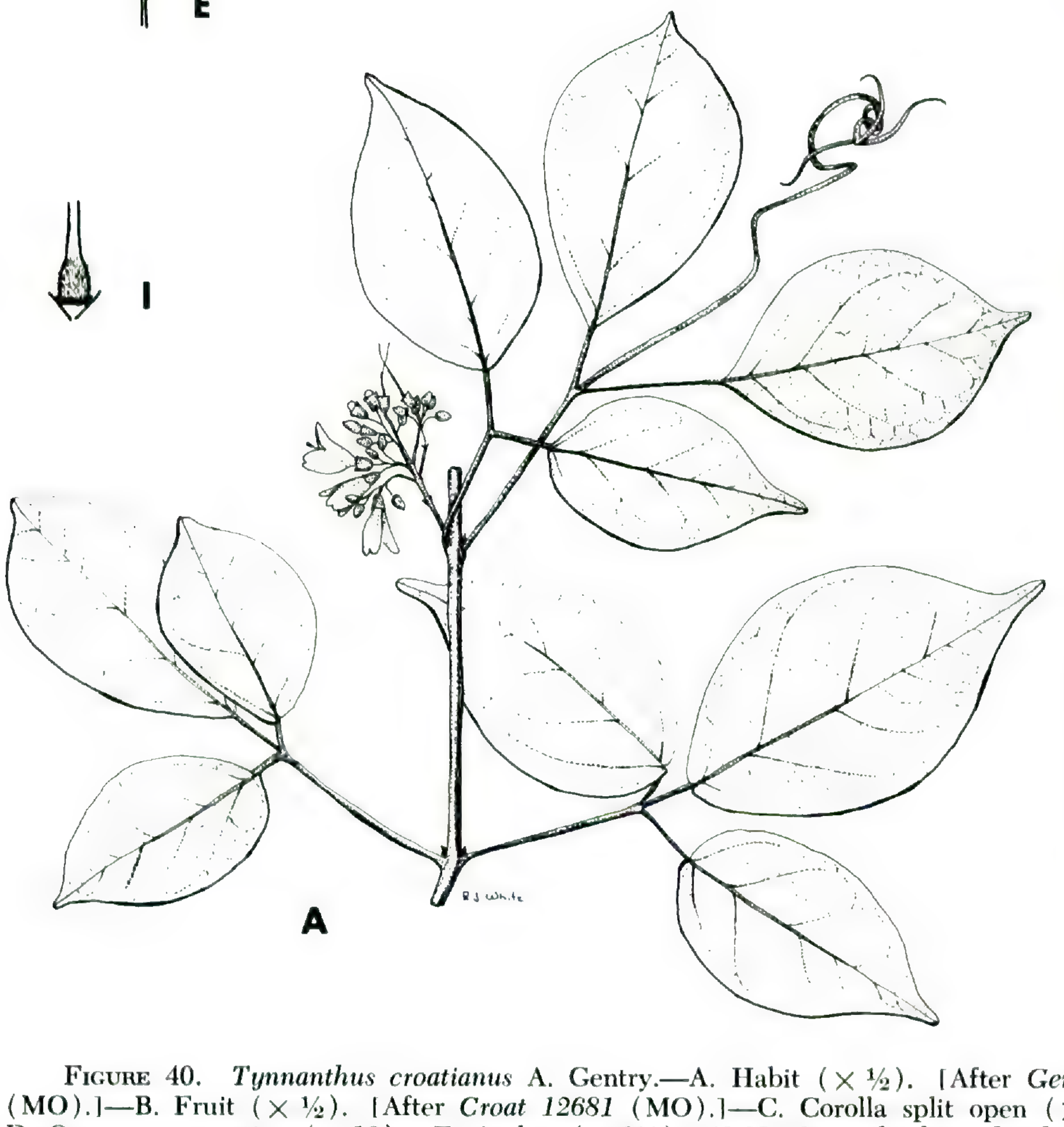


FIGURE 40. *Tynnanthus croatianus* A. Gentry.—A. Habit (× ½). [After *Gentry 5502* (MO).]—B. Fruit (× ½). [After *Croat 12681* (MO).]—C. Corolla split open (× 1¼).—D. Ovary cross section (× 10).—E. Anther (× 6½).—F–H. Front, back, and side views of fresh corolla (× ½).—I. Ovary (× 2½). [After *Gentry 5502* (MO).]

wide, 0.3–0.5 cm thick, the lateral margins somewhat raised, the corners sharply angled, midvein not raised, sparsely to densely pubescent; seeds 0.6–0.8 cm long and 1.7–2.9 cm wide, thin, bialate, the wings hyaline-membranaceous, sharply demarcated from the brown seed body.

A plant of the tropical moist forest, *T. croatianus* is widely but sporadically distributed through central and eastern Panama. It has been collected almost to the Colombian border and probably occurs in that country as well. It flowers during the wet season mostly in July and August. The seeds are wind-dispersed and released during the dry season.

The trifid tendrils, subtetragonal young branchlets, 4-angled, almost cross-shaped pith, and odor of cloves when cut are good recognition characters. The fresh leaves are a glossy yellowish green in color quite similar to those of *Arrabidaea florida*, but the trifid tendril is a sure distinguishing character.

The closest relative of this species is *T. labiatus* (Cham.) Miers, known only from the Sellow type collection and a few other collections from eastern Brazil. Although similar in general facies (calyx size and shape, corolla size, leaf venation), *T. labiatus* differs in its lepidote rather than puberulous inflorescence branches, glabrous leaves, flower color (described as "rosea," *Blanchet 3267*, Fl. Bras. 8(2): 193.), and in having the style glabrous except at extreme base. The great range disjunction between these two species supports their taxonomic separation.

CANAL ZONE: Barro Colorado Island, *Croat 11927, 13975* (both MO, SCZ); *Foster 1178* (MO); *Gentry 708* (MO); *Shattuck 1108* (F, MO, US); *Starry 149* (F, MO). Boy Scout Camp Road, *Croat 12904* (MO); *Gentry 5502* (MO). DARIÉN: Río Balsas between Manene and Tusijuanda, *Duke 13544, 13579* (both MO). El Real, *Gentry 4538* (MO). PANAMÁ: Alhajuela, *Dwyer 1144* (MO, SCZ). Río Pasiga, *Gentry 2203, 2271, 2365* (all MO). 0–4 km from Río Bayano crossing on road to Santa Fé, *Gentry 3875* (MO). Near archeological site at edge of Madden Lake, *Gentry & Tyson 5024* (MO).

42. XYLOPHRAGMA

Xylophragma Sprague *in* Hook., Ic. Pl. *tab. 2770.* 1903. TYPE: *X. pratense* (Bur. & K. Schum.) Sprague.

Lianas; stems with 4 phloem arms in cross section; branchlets terete with conspicuous interpetiolar glandular fields; pseudostipules triangular to ovate, short, acute. *Leaves* 3-foliolate, the terminal leaflet often replaced by a simple tendril. *Inflorescence* a narrow-bracteate, contracted, racemose panicle, axillary on older branchlets. *Flowers* with the calyx cupular, truncate, conspicuously 5-denticulate, usually stellate or dendroid pubescent; corolla lavender, more or less tubular-campanulate, dendroid-puberulous without; anthers glabrous, the thecae straight, divaricate; pollen grains 3-colpate, the exine almost smooth; ovary flattened ovoid, densely lepidote, the ovules 6–8-seriate in each locule; disc cupular-pulvinate. *Fruit* a compressed, woody, ellipsoid capsule, the valves parallel to the septum, more or less smooth or with slightly raised glandular areas, the median nerve not evident, the seeds thin, the wings hyaline-membranaceous, sharply demarcated from the seed body.

Four species of continental tropical America ranging from Mexico to Bolivia, Paraguay, and Brazil.

1. **Xylophragma seemannianum** (Kuntze) Sandw., Kew Bull. 1953: 469. 1954.—FIG. 41.

Bignonia dentata DC. sensu Seem., Bot. Voy. Herald 179. 1854, non DC.
Saldanhaea seemanniana Kuntze, Rev. Gen. Pl. 2: 480. 1891. TYPE: (not seen).
Distictis rovirosana Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 7. 1895. TYPE: Mexico, Tabasco, *Rovirosa 488* (K, US).
Tecoma floccosa Kl. *ex* Bur. & K. Schum. *in* Mart., Fl. Bras. 8(2): 318. 1897. TYPE: British Guiana, *Schomburgk 334* (B, not extant; K, photo).
Adenocalymma cocleense Pittier, Contr. U. S. Natl. Herb. 18: 255. 1917. TYPE: Panama, Coclé, *Williams 522* (NY, US).
Tabebuia floccosa (Kl. *ex* Bur. & K. Schum.) Sprague & Sandw., Kew Bull. 1932: 27. 1932.

Liana to at least 7 cm in diameter, often shrubby when young, the bark relatively smooth with conspicuous raised whitish lenticels, stem with 4 phloem arms in cross section; branchlets subtetragonal to subterete, more or less pubescent with dendroid trichomes, glabrescent, the nodes with interpetiolar glandular fields; pseudostipules inconspicuous or resembling minute bromeliads. *Leaves* 3-foliolate or 2-foliolate with a tendril or tendril scar (some leaves 5-foliolate in *Gentry 1112*, Costa Rica (MO)); leaflets rhombic-ovate to rhombic-obovate, acuminate to acute, truncate to broadly cuneate, 3.5–28 cm long and 1.5–14 cm wide, membranaceous to chartaceous, palmately 3–5-nerved from the base, secondary veins 5–7 on a side, variably lepidote and pubescent above and beneath, beneath with mostly dendroid trichomes, above often with simple trichomes over most of surface and dendroid trichomes on main veins, drying variably olive or brownish; tendril simple, 7–17 cm long; petiolules and petiole dendroid-pubescent, the terminal petiolule 2.1–7 cm long, the lateral petiolules 1.0–2.6 cm long, the petiole 6.4–12 cm long. *Inflorescence* a contracted, lateral raceme or panicle, each flower subtended by 2 narrow bracts, the branches dendroid-pubescent. *Flowers* fragrant with a sweet odor with musky overtones; calyx cupular, 5–9 mm long and 3–5 mm wide, with 5 slender teeth, 1 mm long, pubescent with stellate or dendroid trichomes, especially dense in 5 lines terminating in the marginal teeth, eglandular; corolla lavender outside and on the lobes, the throat white inside, tubular-campanulate, 3.5–6.2 cm long and 1.2–2.0 cm wide at the mouth, the tube 2.2–3.6 cm long, its lower 6–9 mm narrowed to 2 mm wide, the lobes 1.2–2.2 cm long, thickly dendroid pubescent especially in bud outside and on its lobes inside, the tube within mostly glabrous with simple trichomes at and just below the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2.3–3.5 mm long, the longer filaments 1.6–2.1 cm long, shorter filaments 0.9–1.5 cm long, the staminode 1.5–3 mm long, inserted 7–10 mm from the base of the corolla tube; pistil 2.1–2.8 cm long, ovary tapered-cylindrical and somewhat flattened, 1.5–2.5 mm long and 1.5–2 mm wide, densely lepidote, the ovules 6–8-seriate in each locule; disc cupular-pulvinate, 0.5–1 mm long and 1.5–2 mm wide. *Capsule* rounded-oblong, flattened, 5.5–16 cm long and 3.4–5 cm wide, 1–1.5 cm thick, drying dark, inconspicuously lepidote, often with raised glandular areas; seeds

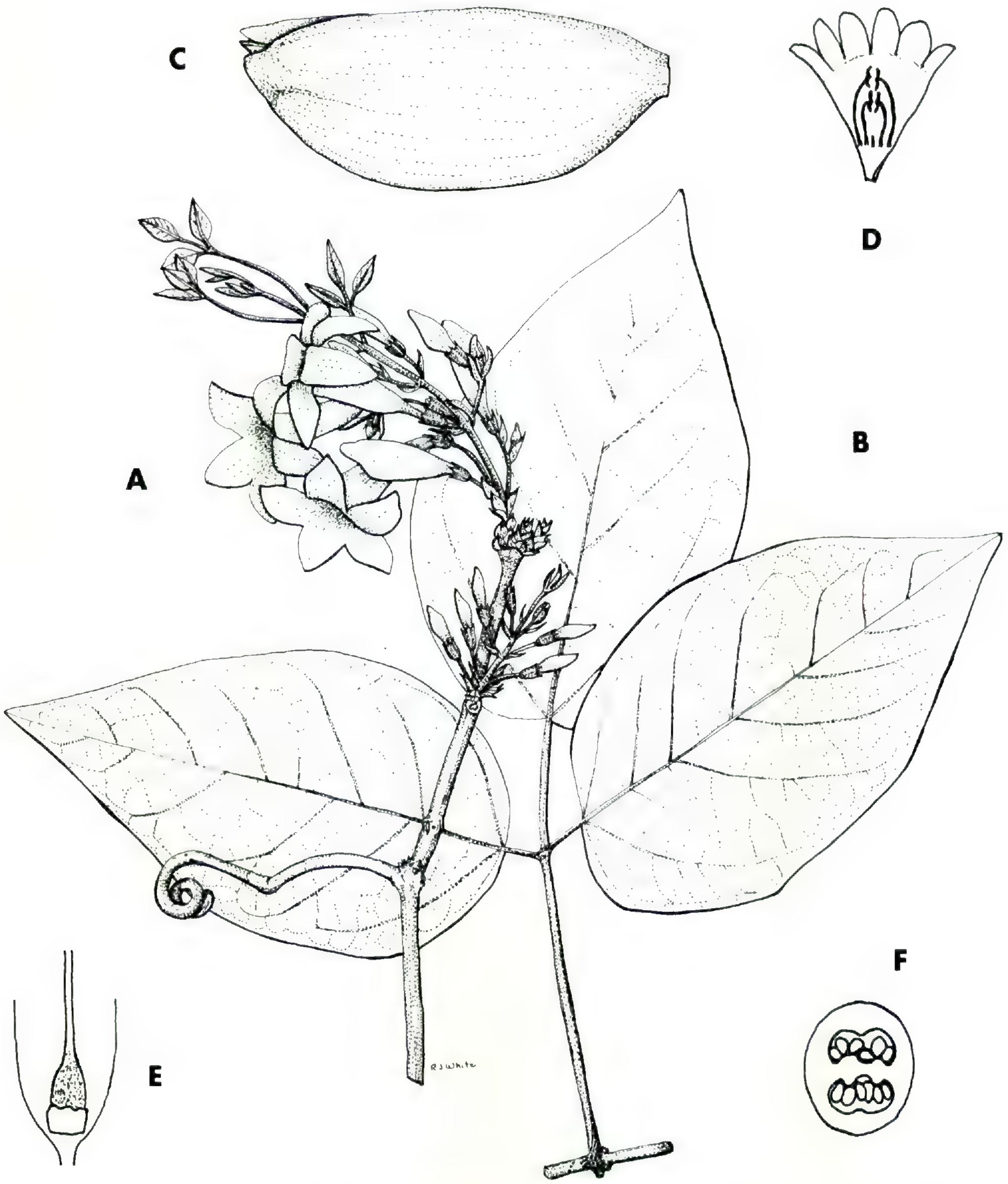


FIGURE 41. *Xylophragma seemannianum* (Kuntze) Sandw.—A. Habit (× ½). [After *Porter et al. 5150* (MO).]—B. Leaf (× ½). [After *Gentry 3776* (MO).]—C. Fruit (× ½). [After *Gentry 4965* (MO).]—D. Corolla split open (× ½).—E. Ovary and disc (× 3).—F. Ovary cross section (× 9). [After *Gentry 3890* (MO).]

1.6–2.9 cm long and 3.0–5.2 cm wide, the wings hyaline-membranaceous, sharply demarcated from the seed body.

A common vine of tropical dry forest, premontane moist forest, and drier parts of the tropical moist forest, *Xylophragma seemannianum* becomes progressively less common in wetter parts of the tropical moist forest. It ranges from Mexico to Guyana. This species flowers during late dry season from

March to May. The fruits take about a year to mature, releasing seeds during the next dry season.

Although first described as a species of *Saldanhaea*, this plant is quite distinct from that genus, which I have united with *Cuspidaria*. The fruit is different from the relatively narrow, elongate fruit of *Cuspidaria* and lacks any hint of raised margins or submarginal area. This species also lacks the distinctive bent anther thecae and pollen tetrads of *Cuspidaria* (including *Saldanhaea*).

Xylophragma seemannianum is distinguished from other species with which it might be confused by the dendroid trichomes of its leaves and petioles. In the field this pubescence assumes a macroscopically characteristic mealy form. The combination of interpetiolar glandular fields and relatively large leaves also serves to mark this species.

The generic name, meaning woody partition, refers to the woody capsule valves and comes from the Greek. It is neuter and the specific epithet *seemannianum* thus takes the neuter ending used here rather than the feminine gender given it by Sandwith (Kew Bull. 1953:469. 1954).

CANAL ZONE: Barro Colorado Island, *Croat 5029* (SCZ), *Croat 13962* (MO, SCZ); *Foster 705, 798* (both PMA). Victoria Fill near Miraflores Locks, *Allen 1755* (F, GH, MO, US). Road C25B, E of Madden Forest, *Croat 15265* (MO). Pipeline Road, *Croat 9327* (MO, SCZ); *Gentry 1582, 4857* (both MO). Curundu, *Gentry 1601* (MO). Boy Scout Camp road near Madden Lake, *Gentry 2051* (MO). Farfan beach road, *Gentry 4903* (MO). N of Paraíso, *Gentry 4960* (MO). C-29 beyond Summit Gardens, *Harvey 5286* (F). Along Las Cruces Trail in Madden Forest, *Lewis et al. 5304* (MO, NY, SCZ). Gamboa district, *Maggs II-44* (F, K). Gorgona, *Seemann 603* (BM, K). CHIRIQUÍ: Remedios, *Lindsay 468* (F). COCLÉ: Penonomé and vicinity, *Williams 522* (NY, US). DARIÉN: Cerro Piriaque, *Duke 8115* (MO). Río Tuira between Ríos Punusa and Mangle, *Duke 14583* (MO). Santa Fé, *Gentry 4310* (MO). Río Tuira between Ríos Pucuro and Paya, *Gentry 4329* (MO). Near village of Paya, *Gentry 4396* (MO). El Real, *Gentry 4547* (MO). Trail from Cerro Pirre to El Real, *Gentry 4783* (MO). Cerro Piriaque, *Tyson et al. 3824* (MO, SCZ). HERRERA: E of Las Minas, *Gentry 3140* (MO). PANAMÁ: Perlas Islands, Isla de La Bayonetta, *Dwyer 1756* (MO). Near Capira, *Allen 730* (GH, MO, US). Dam site on Río Bayano, *Gentry & Tyson 1663A* (MO). Río Maestro, *Gentry 2225* (MO). Río Pasiga, *Gentry 2261, 2262, 2264, 2276* (all MO). Río Piragua (Tabardí), *Gentry 2575* (MO). Icantí, *Gentry 2608* (MO). Near Río Espavé, *Gentry 3739* (MO). Trail from Río Espavé toward Río Agua Clara, *Gentry 3776* (MO). 10–15 km from Río Bayano crossing on trail to Santa Fé, *Gentry 3822, 3886* (both MO). Río Espavé near junction with Río Bayano, *Gentry 3890* (MO). W of Cañitas, *Gentry 4965* (MO). E of Cañitas, *Gentry 4975* (MO). Between Chepo and El Llano, *Gentry & Tyson 1638, 1688* (both MO). Río Cabra, *Maurice 764* (US). Between Río Pacora and Chepo, *Porter et al. 5150* (MO, SCZ). E of Río Tocumen, *Standley 26589* (GH, US). Vicinity of Capira, *Woodson et al. 1310* (MO). VERAGUAS: S of Santa Fé, *Gentry 2935* (MO).

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